

Table of Contents

Commonness and Rarity: Theory and Application of a New Model to Mediterranean Montane Grasslands

<u>ABSTRACT</u>	0
<u>INTRODUCTION</u>	1
Theories.....	2
<u>MATERIALS AND METHODS</u>	4
<u>RESULTS</u>	7
<u>Local characteristics</u>	7
<u>Ecological breadth groups</u>	9
<u>Geographic range</u>	11
<u>Categorization</u>	13
<u>DISCUSSION</u>	14
<u>Conservation implications</u>	15
<u>Tests of the theories</u>	15
<u>Speculations</u>	15
<u>RESPONSES TO THIS ARTICLE</u>	17
<u>Acknowledgments</u>	17
<u>LITERATURE CITED</u>	17
<u>APPENDICES</u>	20

Commonness and Rarity: Theory and Application of a New Model to Mediterranean Montane Grasslands

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- [Abstract](#)
- [Introduction](#)
 - ◆ [Theories](#)
- [Materials and Methods](#)
- [Results](#)
 - ◆ [Local Characteristics](#)
 - ◆ [Ecological Breadth Groups](#)
 - ◆ [Geographic Range](#)
 - ◆ [Categorization](#)
- [Discussion](#)
 - ◆ [Conservation Implications](#)
 - ◆ [Tests of the Theories](#)
 - ◆ [Speculations](#)
- [Responses to this Article](#)
- [Acknowledgments](#)
- [Literature Cited](#)
- [Appendices](#)
 - ◆ [Appendix 1. Site by species data matrix](#)
 - ◆ [Appendix 2. Ecological information for the 232 species](#)
 - ◆ [Appendix 3. Environmental variables measured and ordination axis positions for the 92 plots](#)
 - ◆ [Appendix 4. Details of multivariate methods](#)

ABSTRACT

We examined patterns of commonness and rarity among plant species in montane wet grasslands of Iberia. This examination is set within two contexts. First, we expanded on an earlier scheme for classifying species as common or rare by adding a fourth criterion, the ability of that species to occupy a larger or smaller fraction of its potential suitable habitats, i.e., habitat occupancy. Second, we explicated two theories, the superior organism theory and the generalist/specialist trade–off theory. The data consisted of 232 species distributed among 92 plots. The species were measured for mean local abundance, size of environmental volume occupied, percentage of volume occupied, range within Iberia, and range in Europe and the Mediterranean basin. In general, all measures were positively correlated, in agreement with the superior organism theory. However, specialist species were also found. Thus, patterns of commonness and rarity may be due to a combination of mechanisms. Analyses such as ours can also be used as a first step in identifying habitats and species that may be endangered.

INTRODUCTION

Why are some species common and others rare? This question is at the heart of much ecological research and has reached special prominence with current concerns over species conservation and global change (Kunin and Gaston 1997). In this paper, we examine patterns of commonness and rarity among plant species in montane wet grasslands at local, regional, and continental scales. We propose a new conceptual model and apply it to field data. In doing so, we expand on current ideas about commonness and rarity and examine the predictions of two theories.

A touchstone for current discussions of commonness and rarity is the scheme by Rabinowitz (1981), who pointed out that there are actually many forms of rarity ([Table 1A](#)). She classified species based on three criteria: geographic range (wide or narrow), habitat specificity (broad or restricted), and local abundance (somewhere large or everywhere small). Only one of the eight possible combinations (wide range, broad habitat specificity, and somewhere large local abundance) is classified as common. The other seven each include some form of rarity, and some of them are even questioned to exist. For an in–depth discussion of types of rarity, see Gaston (1994).

Table 1. A scheme for describing types of commonness and rarity.

A) The original proposal by Rabinowitz (1981).

Geographic range	Wide		Narrow	
Habitat specificity	Broad	Restricted	Broad	Restricted
Abundance somewhere large	Common	Predictable	Unlikely	Endemics
Abundance everywhere small	Sparse		Non–existent	

B) Our new scheme adding the notion of habitat occupancy.

Geographic range	Wide				Narrow			
Habitat specificity	Broad		Restricted		Broad		Restricted	
Abundance	Large	Small	Large	Small	Large	Small	Large	Small
Habitat occupancy high	Common	Widespread	Indicator		Locally common	Non–existent	Endemic indicator	
Habitat occupancy low	Highly dispersed	Sparse	Locally endangered		Potentially endangered		Endangered	

There is yet a fourth criterion for defining commonness vs. rarity. Within the habitat specificity of a species is the ability of that species to occupy a larger or smaller fraction of its potential suitable habitats, i.e., habitat occupancy. This criterion is theoretically independent of the other three ([Table 1B](#)). As far as we are aware, no study has simultaneously examined the relationship among all four criteria. For example, *Agrostis castellana* is found in a range of mesic forests and grasslands including those of our study. Yet, within *Quercus pyrenaica* forests in the same area, this species was found in only two of 21 plots (Fernández González 1991). In contrast, *Carex demissa* is a specialist of wet grasslands and was found within 63% of those habitats in our study (see *Results*). The distinction between habitat occupancy and habitat specificity is somewhat akin to the distinction between realized and fundamental niche (Hutchinson 1957). We emphasize, though, that this is just a rough analogy, because habitat specificity is measured as the observed distribution of a species. Although the notion of occupancy has been raised previously (e.g., Orians 1997), ours is the first study to analyze its relationship to all of these other components of rarity (however, see Burgman 1989).

For convenience, we modify and expand Rabinowitz's (1981) earlier scheme. Now, only one of the 16 combinations of species characteristics ([Table 1B](#)) would be considered common: wide geographic range, broad habitat specificity, large local abundance, and frequent habitat occupation. According to Rabinowitz, the other categories are all forms of rarity. We disagree somewhat by recognizing a category of locally common species, similar to common species but having a narrow geographic range. Species in the categories that we designate as widespread and highly dispersed could also reasonably be considered common. These quibbles, however, do not obviate Rabinowitz's central point that commonness and rarity are complex phenomena. Of course, nature does not fit into neat categories. This binary classification scheme actually stands for a continuum of species types.

The use of wet grasslands is particularly appropriate in this context. These habitats differ from the surrounding land because groundwater seeps result in a moister environment, changes in soil features, and a distinctive plant community. These differences are most conspicuous in the dry season, when patches of green, wet-meadow vegetation, dominated by *Juncus*, *Carex*, and hygrophYTE graminoid species, stand out against a yellow-brown matrix of senescent annual grasses.

These habitats are rare throughout the Mediterranean region, where they represent important islands of biodiversity (Bernáldez et al. 1993, Rey Benayas et al. 1998). In the mountains of central Spain, they occupy only 9% of the total land area. However, these habitats are much richer in species than are the surrounding plant communities, holding 43.3% of the perennial species in these systems because of the presence of outcropping water in the summer (García Sánchez-Colomer 1998). Also, their species richness per unit area is greater (24.9 species/100 m² vs. 16.4 species/100 m²; Rey Benayas et al. 1998). Understanding their species composition and why and how they act within the overall context of species' ranges and habitat spectra will help us to design and manage other sorts of diversity islands, either natural or man-made, by fragmentation of former continuous habitats.

Theories

If we are to be successful both in understanding commonness and rarity and in using that knowledge, we must be able to place our information in a theoretical context. Theories are necessary to organize our data and to guide future actions. Currently, we have few general theories about species richness, commonness, and rarity. Most of what go by the name of theory are merely empirical generalizations. Some seem to hold up well to scrutiny (e.g., island biogeography hypotheses; McGuinness 1984, Myers and Giller 1988), whereas others have been called into question (e.g., Rapoport's rule; Rapoport 1982, Stevens 1989, Pagel et al. 1991, Hughes et al. 1996). We explore two theories that purport to explain patterns of commonness and rarity, testing the predictions of each. Both theories have the virtue of starting from the biology of the organism and deriving ecological patterns. Thus, they are mechanistic models rather than simply empirical generalizations.

The first theory is that of Brown (Brown 1984, Brown et al. 1995), which we term the superior organism theory. He begins with the premise that species vary in their abilities to exploit nature. Some species have large fundamental niches, whereas others have narrow ones. Next, he proposes that the center of a species' range is the region where it can exploit the widest range of resource combinations and, therefore, habitats. Here, the species will be at high abundance. As the distance from this center increases, because environmental variables are autocorrelated, the conditions favoring the species become rarer. Its local habitat specificity narrows and its abundance decreases. Eventually, the edge of the geographic range is reached. Those species that begin with a broad niche will have a large geographic range, whereas those with narrow niches will have a small geographic range.

The second theory is the older notion of a generalist/specialist trade-off (e.g., Fox and Morrow 1981, Futuyuma and Moreno 1988). Again, species vary from having broad to narrow niches. However, this habitat specificity exists throughout the geographic range of a species, rather than narrowing toward the edge of the range. Moreover, habitat specificity trades off with local abundance. Where they are found, specialists have high abundances and generalists have lower abundances.

These two theories make alternative predictions concerning patterns of commonness and rarity ([Table 2](#)). In its most extreme form, the superior organism theory predicts the existence of two categories: (1) superior species with wide geographic ranges, broad habitat specificity, large local abundances, and high occupancies; and (2) inferior species with the opposite combination. In [Table 1B](#), these categories are termed common and endangered. The trade-off theory also predicts two categories: (1) generalist species with wide geographic ranges, broad habitat specificity, small abundances, and low occupancies; and (2) specialist species with the opposite combination. In [Table 1B](#), these categories are termed sparse and endemic indicators. Of course, both theories allow for intermediate types, but not for all possible combinations of species traits. For example, neither theory predicts the existence of species with narrow geographic ranges and broad habitat specificities, which we termed locally common. For correlations among traits, the superior organism theory predicts positive correlations between geographic range, habitat specificity, local abundance, and habitat occupancy (Gaston and Lawton 1990, Lawton et al. 1994). In contrast, the trade-off theory predicts positive correlations between geographic range and habitat specificity, positive correlations between local abundance and habitat occupancy, and negative correlations between the first group and the second group.

Table 2. Predictions of the superior organism and trade-off theories. Those predictions upheld by the data are shown in **boldface**. Ecological breadth groups: WGS, wet-grassland specialists; WGG, wet-grassland generalists; MHG, mesic-habitat generalists.

	Theory	
Superior organism	Trade-off	
Most frequent categories	Common and endangered	Sparse and endemic indicators
A) Correlations among traits		
Geographic range and local abundance	positive	negative
Habitat specificity and local abundance	positive	negative
Habitat specificity and habitat occupancy	positive	negative
B) Ordering of ecological breadth groups		
Geographic range	MHG>WGG>WGS	MHG>WGG>WGS
Habitat specificity	WGS=WGG>MHG	MHG>WGG>WGS
Local abundance	WGS=WGG>MHG	WGS>WGG>MHG
Habitat occupancy	MHG>WGG>WGS	WGS>WGG>MHG

An alternative way to consider these local distributions is by first classifying the species based on their species-wide habitat specificity (i.e., ecological breadth). For example, we can classify the wet-grassland species as (1) those that are narrowly specialized to just part of these habitats; (2) those that are found across all types of wet grasslands, but not beyond them; and (3) those that are found across a wide range of mesic habitats, including wet grasslands. Both theories allow for such an array of species. However, the theories make alternative predictions about values of geographic range, habitat specificity, local abundance, and habitat occupancy across these groups ([Table 2](#)). The superior organism model predicts that the third group of species will have the greatest geographic range and the highest occupancy. The second and first groups will have progressively lower values for these traits. Habitat specificity within this circumscribed set will be equally high for the first and second groups and lower for the third group. Finally, local abundance will be high for the first and second groups because these habitats are central for these species. In contrast, the trade-off model predicts that local abundance and habitat occupancy will be highest for the first group and progressively lower for the second and third groups. For habitat specificity, it predicts that the third group will be highest, and progressively smaller for the second and first group. Finally, it makes the same prediction as the other theory with respect to the relative rankings of geographic range.

MATERIALS AND METHODS

The study sites consisted of 66 wet-grassland habitats spread among 2069 km² in the Sierra de Guadarrama of central Spain (40° N and 4° W; [Figs. 1](#) and [2](#)). The climate is mediterranean. Altitude ranges from 560 to 2430 m, mean annual temperature ranges between 12.4 and 6.3 °C, and total annual precipitation ranges between 456 and 1331 mm. The parent material is mostly granite. We used panchromatic aerial photographs to map the network of wet-grassland habitats in the study area. We selected recent 1:20000-scale stereopairs to generate an updated, accurate map of these habitats. Within them we placed 92 100-m² plots. Plot locations were chosen to maximize the environmental range sampled. They were placed after field inspections so that larger grasslands with more than one habitat zone (based on visual inspection) received more plots. Most of the wet grasslands (66.7%) received one plot, with a maximum of four plots in one grassland. For small grasslands with only one obvious habitat zone, the plot was placed in the center. For larger grasslands, plots were placed in the approximate center of each habitat zone.

Fig. 1. Map of the study area and location of sample plots in wet grasslands of the Sierra de Guadarrama, Spain.

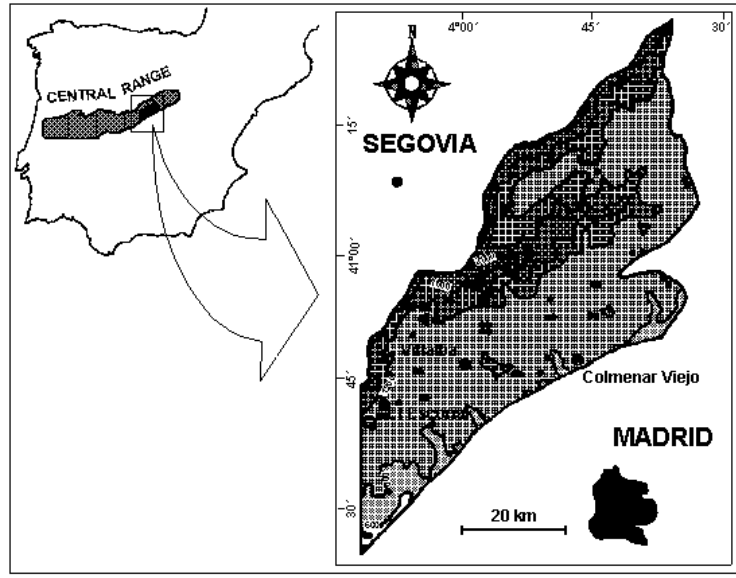


Fig. 2. A sedge–rush habitat in La Salabrosa, Madrid, dominated by *Scirpus holoschoenus*. The photograph shows the contrast between this wet habitat, due to groundwater seepage, and the surrounding habitats dominated by evergreen oaks (*Quercus ilex* subsp. *rotundifolia*) and xerophytic annuals.



We surveyed all perennial vascular plants occurring in the sample plots ([Appendices 1](#) and [2](#)). Over 90% of species in these habitats are perennials. A total of 237 taxa were found, of which 232 could be identified to species. The four species characteristics of local abundance, habitat specificity, habitat occupancy, and geographic range were measured as follows. (See [Table 3](#) for definitions of all measures.) Abundance was estimated by eye using a six–point Braun–Blanquet scale (0, 0.1 = <1% cover, 1 = 1%–10% cover, 2 =

10%–25% cover, 3 = 25%–50% cover, 4 = 50%–75% cover, 5 = 75%–100% cover). Our measure of local abundance was the mean cover value for all plots within which the species appeared. Although Rabinowitz's scheme can be construed to refer to maximal abundance, the mean and the maximum were highly correlated for our data ($r_s = 0.88$, $P < 0.0001$, $n = 232$).

Table 3. Definitions of the ecological measures used for each species.

Ecological measure	Definition
Environmental volume	Three-dimensional range of a species in an ordination space based on 53 environmental measures for each of 92 plots. The range on each axis was the distance of the sites with the largest and smallest axis scores that contained that species.
Abundance	Mean cover value of a species, based on a six-point Braun–Blanquet scale, for all plots in which the species appeared.
Ecological breadth	Classification of each species into one of four groups based on its general distribution: wet–grassland specialist (WGS), wet–grassland generalist (WGG), mesic–habitat generalist (MHG), and generalist (G).
Wet–grassland specialists	Species characteristic of Iberian Atlantic climates.
Wet–grassland generalists	Species that are found in a range of mesic habitats.
Mesic–habitat generalists	Species that are found in a range of mesic habitats.
Generalists	Species that are typically found in nonwetland habitats.
Habitat occupancy	The percentage of plots within an environmental volume that were occupied by a given species.
Regional range	The extent of a species' range within the Iberian Peninsula, in km ² .
Continental range	The number of geographic units across Europe and the Mediterranean basin with a recorded presence for a species.

Habitat specificity was measured at two scales: environmental volume and ecological breadth. Environmental volume measured habitat specificity within the set of sample plots in the wet grasslands. Ecological breadth measured it across a species' range. Environmental volume was calculated as follows. In each plot, we recorded 53 variables ([Appendix 3](#)) that were ultimately reduced into a three-dimensional, multivariate space, the first three eigenvectors from a principal components analysis. For each plant species, the environmental volume was the rectangular solid determined by the maximum and minimum coordinates on all three axes. See [Appendix 4](#) for details.

For ecological breadth, each species was classified into one of four groups: wet–grassland specialist (WGS), wet–grassland generalist (WGG), mesic–habitat generalist (MHG), and generalist (G). The first three groups consist of species whose typical habitat is contained within the group of sampled plots. Wet–grassland specialists are characteristic of Atlantic climates. In our study, they were found only in the high–elevation plots because those plots receive the highest amounts of precipitation and have the lowest potential evapotranspiration.

Wet–grassland generalists are potentially found in all of the sampled sites, but would not be found in other habitats. Mesic–habitat generalists are also found in other mesic habitats such as deciduous forests (*Quercus pyrenaica* associations) and coniferous forests (*Pinus sylvestris* associations). Generalist species are typically not found in these habitats and, thus, are at the edge of their habitat ranges. This classification scheme was made independently of the data and was based on the flora and habitat descriptions in Rivas Martínez (1963), Tutin et al. (1964, 1968, 1972, 1976, 1980), Bolós and Vigo (1984, 1990, 1996), Valdés et al. (1987), and Fernández González (1991).

Habitat occupancy was based on each species' environmental volume. For each species, the number of plots within its volume was determined. Habitat occupancy was calculated as the percentage of plots within the volume that were occupied. This measure assumes that, for each species, all habitats intermediate to those already occupied are suitable.

Geographic range was measured at two scales: regionally across the Iberian Peninsula, and continentally across Europe and the Mediterranean basin. For both measures, we used published distribution maps and lists. At the regional scale, geographic range was measured as the extent of the range within the Iberian Peninsula in km². These regional ranges were taken from the maps of Bolós and Vigo (1984, 1990, 1996) and Hultén and Fries (1986) and were determined by scanning the maps using a Tamaya Digitizing Area–Line Meter (Tamaya Technics, Tokyo, Japan). At the continental scale, geographic range was measured as the number of geographic units with a recorded presence for the species. Data were from Tutin et al. (1964, 1968, 1972, 1976, 1980), Hultén and Fries (1986), and Greuter et al. (1984). These sources define 49 geographic units that are variously entire countries, groups of countries, or smaller units such as discrete islands. Although this measure of continental range does not correct for size differences among geographic units, it suffices as a general measure of continental range.

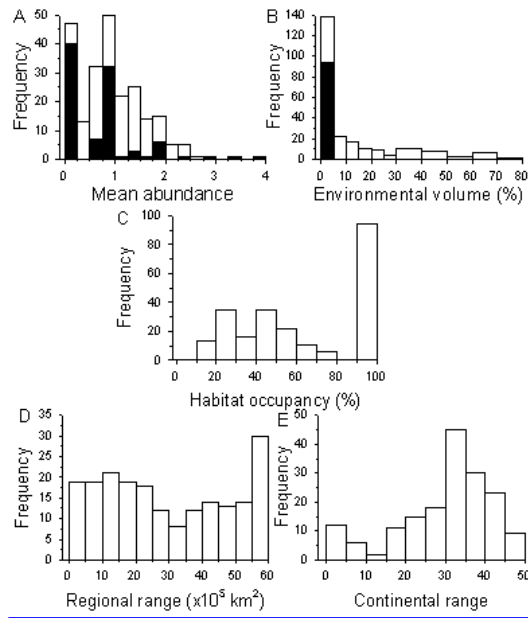
Data were analyzed using Systat (SYSTAT 6.1 for Windows, SPSS, Chicago, Illinois, USA). The measures of local abundance, environmental volume, and habitat occupancy were not normally distributed. Thus, all analyses were done as nonparametric tests.

RESULTS

Local characteristics

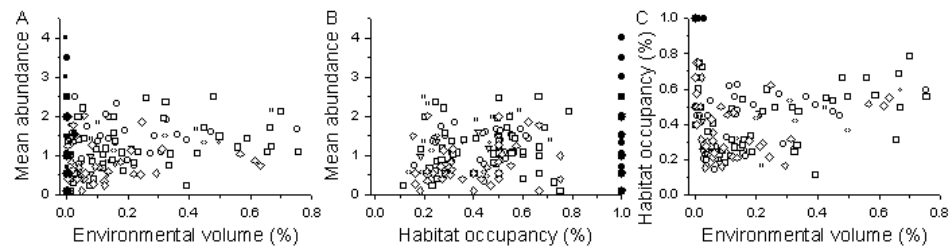
The distribution of site occupancy by species shows a typical log–normal distribution, with 29% of the species in one plot only and 17% of the species in two plots. Most species had low local abundances and small environmental volumes ([Fig. 3](#)). On average, species occupied about half of the plots within their environmental volumes. We next examine the relationships among the variables and refer the reader to [Table 2](#) for predictions of the two theories.

Fig. 3. Frequency histograms of (A) mean abundance, (B) environmental volume, (C) habitat occupancy, (D) regional range, and (E) continental range for 237 plant species sampled in the wet grasslands of the Sierra de Guadarrama. In (A) and (B), solid bars correspond to species with 100% of their environmental volumes occupied; open bars correspond to species with <100% of their environmental volumes occupied.



Local abundance and environmental volume were positively correlated ([Fig. 4A](#)). The situation was more complicated for correlations with habitat occupancy, however. When all species were included in the analyses, both local abundance and environmental volume were negatively correlated with habitat occupancy ([Figs. 4B,C](#)). The negative correlations were due, however, to the large number of species found in only one or two sites. A species that appears in a single plot perforce must occupy 100% of its volume. Similarly, most species found in only two plots, and occasionally in three plots, also had 100% occupancies. This large group of species had the potential to distort the analysis. When those 94 species were removed, the correlation with habitat occupancy became positive for local abundance ($r_s = 0.20$, $P < 0.02$, $n = 138$) and disappeared for environmental volume ($r_s = 0.02$, $P > 0.5$, $n = 138$). The species found in only one or two plots had a range of abundances from small to large. Otherwise, species with broader local habitat specificities tended to have higher abundances where present.

Fig. 4. Relationships among mean abundance, environmental volume, and habitat occupancy. Symbols indicate the ecological breadth group: *triangle*, WGS; *circle*, WGG; *square*, MHG; and *diamond*, G. Solid symbols correspond to those species with 100% of their environmental volumes occupied; open symbols correspond to those species with < 100% of their environmental volumes occupied. Correlations and statistical significance are given in [Table 5](#).



Ecological breadth groups

The relationship between these three traits (environmental volume, local abundance, and habitat occupancy) and ecological breadth was more complex ([Table 4](#)). Again, see [Table 2](#) for the theory predictions. First, we considered environmental volume, which tells us whether we were successful in our classification of specialists and generalists. As expected, on average, mesic–habitat generalists had the largest volumes, followed by wet–grassland generalists, then generalists, and finally wet–grassland specialists.

Table 4. Species characteristics of environmental volume, local abundance, habitat occupancy, and geographic range of Spanish montane grassland species as a function of their ecological breadth (WGS, wet–grassland specialists; WGG, wet–grassland generalists; MHG, mesic–habitat generalists; G, generalists; defined in [Table 3](#)). Volumes are expressed as a percentage of the maximum possible. Differences among groups were determined by a Kruskal–Wallis nonparametric ANOVA and Dunn's nonparametric post hoc test (Zar 1984: 200). Statistically significant ($\alpha = 0.05$) differences among groups are indicated by different superscripts.

	Ecological breadth group				Statistics	
	WGS	WGG	MHG	G	Chi2	<i>P</i>
Environmental volume						

	range	(0.0–21)	(0.0–75)	(0.0–7
	no. species	28	71	66
Mean abundance				
	median	1.00 ^a	1.10 ^a	1.00 ^a
	range	(0.1–2.0)	(0.1–4.0)	(0.1–2
	no. species	28	71	66
Habitat occupancy				
	median	100.0	55.2	55.4
	range	(18–100)	(14–100)	(11–10
	no. species	28	71	66
Regional range (x10 ⁵ km ²)				

Continental range	median	1.40 ^c	2.19 ^{bc}	2.80 ^a
	range	(0.08–5.81)	(0.25–5.81)	(0.29–5.81)
	no. species	28	66	53
	median	33	33	34
	range	(7–48)	(3–48)	(4–47)
	no. species	27	56	48

For mean abundance, generalists had significantly lower mean abundances than species in the other three categories. Of the generalists, 36% had the lowest mean abundance possible, 0.1. Thus, these habitats were marginal for the generalist species, as might be expected.

Habitat occupancy did not differ among groups. This trait was unrelated to habitat specificity. When species with 100% habitat occupancy were eliminated, median occupancy was 27%, 44%, 48%, and 40% for the four groups, respectively. Again, they did not differ (chi-square = 4.83, $P = 0.18$).

Next, we examined correlations among local abundance, environmental volume, and habitat occupancy within each group. When all species were included, all correlations had the same sign as the overall correlations ([Table 5](#)). Local abundance and environmental volume were positively correlated, whereas both were negatively correlated with habitat occupancy. The only notable variation among groups was the substantially lower correlation of local abundance and environmental volume for wet-grassland specialists. Thus, in general, the ecological specificity of a species did not alter the tendency for broader local habitat specificity to be associated with higher abundance.

Table 5. Spearman rank correlations among local abundance, environmental volume, habitat occupancy, and regional ranges across over all species ($n = 232$) and for groups of Spanish montane grassland species based on their ecological breadth, as defined in [Table 3](#). For the overall correlations, "Excluded" indicates species with 100% occupancy deleted ($n = 138$). Groups are as in [Table 3](#). Correlations that differ significantly from zero ($\alpha = 0.05$) are indicated in boldface. Sample sizes for ecological breadth groups are given in [Table 2](#).

Traits	Overall		Ecological breadth group			
	All	Excluded	WGS	WGG	MHG	G
Abundance–volume	0.41	0.33	0.02	0.40	0.47	0.57

Abundance–occupancy	–0.22	0.20	–0.10	–0.17	–0.18	–0.46
Abundance–regional range	–0.09	–0.12	–0.05	–0.07	0.12	0.16
Abundance–continental range	0.17	0.07	–0.07	0.11	0.15	0.44
Volume–occupancy	–0.75	0.02	–0.86	–0.69	–0.58	–0.83
Volume–regional range	0.24	0.14	0.13	0.05	0.41	0.27
Volume–continental range	0.28	0.14	0.08	–0.09	0.42	0.51
Occupancy–regional range	–0.26	–0.05	–0.40	–0.09	–0.29	–0.29
Occupancy–continental range	–0.24	–0.04	–0.06	0.01	–0.34	–0.42
Regional–continental range	0.46	0.64	0.33	0.35	0.64	0.54

Geographic range

We next considered the two measures of geographic range: regional and continental. The two measures were correlated with each other ($r_s = 0.46$, $P < 0.001$, $n = 163$; [Fig. 5](#)). Both regional and continental range were positively correlated with environmental volume and negatively correlated with habitat occupancy ([Figs. 6 and 7](#)). In contrast, for local abundance, regional range was not correlated, whereas continental range was positively

correlated. All of these correlations were nonsignificant when the species with 100% occupancy were removed, although the signs of the correlations remained the same. For the other measure of habitat specificity, ecological breadth, the rank order with regard to regional range was as expected. Specialist species had the smallest regional ranges, followed by wet–grassland generalists, then mesic–habitat generalists, and, finally, generalist species had the largest ranges ([Table 4](#)). The groups did not differ, however, in continental ranges.

Fig. 5. Relationship between regional range and continental range. Correlations and statistical significance are given in [Table 5](#).

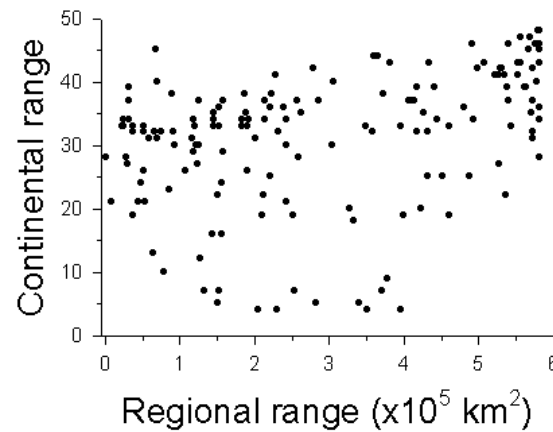


Fig. 6. Relationships between regional range and (A) mean abundance, (B) environmental volume, and (C) habitat occupancy. Correlations and statistical significance are given in [Table 5](#).

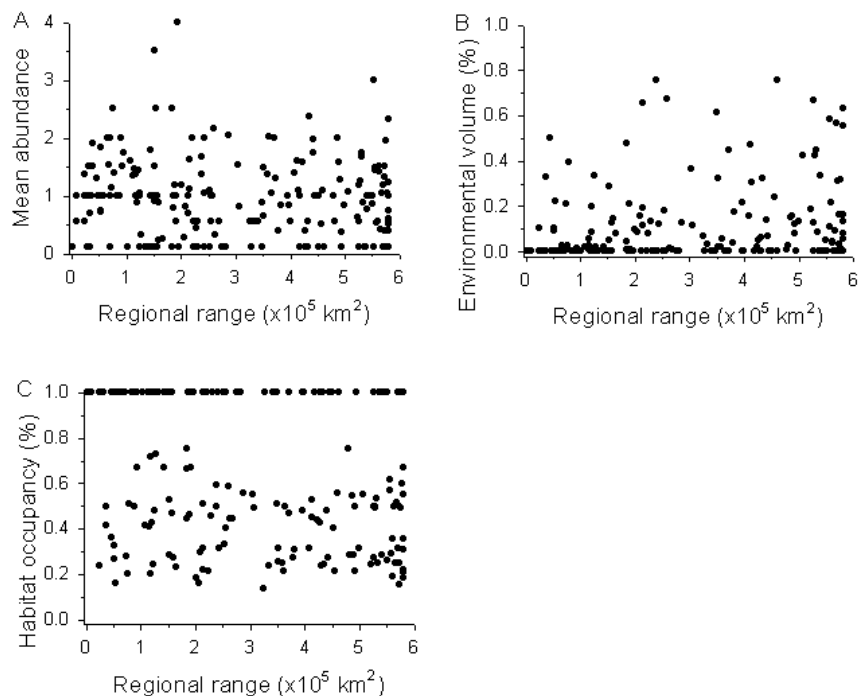
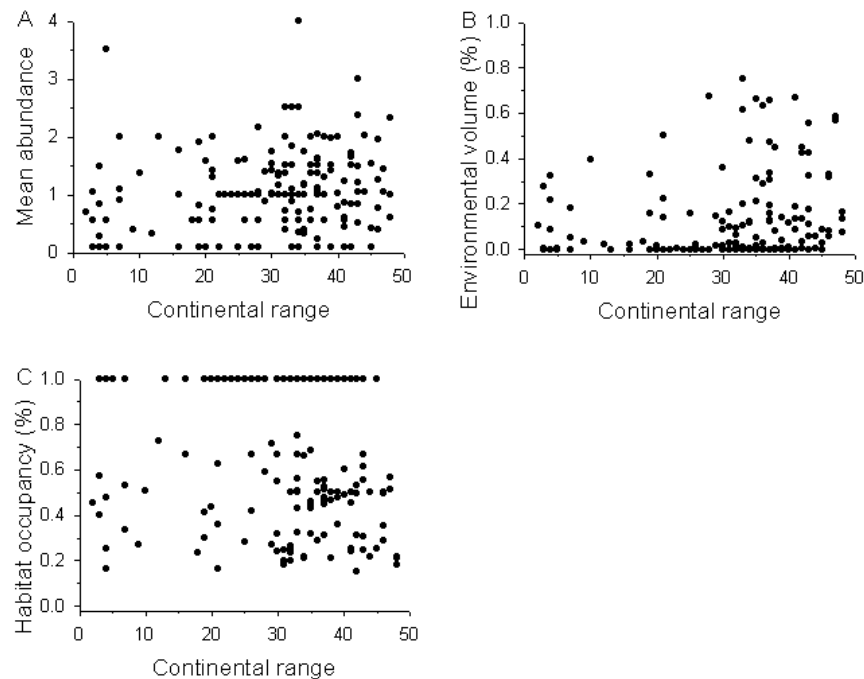


Fig. 7. Relationships between continental range and (A) mean abundance, (B) environmental volume, and (C) habitat occupancy. Correlations and statistical significance are given in [Table 5](#).



Categorization

To explore more completely the patterns of commonness and rarity, we dichotomized the data to fit within the scheme shown in [Table 1B](#). Although such a procedure subsumes information within the categories, it allows a multivariate view of the data. We dichotomized the data using the approximate median of each distribution: geographic range wide = present in at least 35 geographic units, habitat specificity broad = environmental volume at least 11% of total, habitat occupancy high = more than 40%, local abundance large = maximal abundance at least 2.

Species were not evenly distributed among the 16 categories ([Table 6](#)), being overrepresented among categories that included high habitat occupancy. The most frequent category was endemic indicator species with small abundances (36%), followed by common species. The least frequent categories were the four with a broad habitat specificity and small local abundance. Two additional categories differing in local abundance (wide geographic range, restricted habitat specificity, and low habitat occupancy) also included few species. Only one category (narrow geographic range, broad habitat specificity, small abundance, and high occupancy) had no species.

Table 6. Percentage of species sampled in montane wet grasslands that were found within each category of our scheme described in [Table 1B](#). The upper value is for all species ($n = 220$) and the lower value is for wet-grassland specialists and generalists only ($n =$

96). See text for the threshold values that were used to dichotomize the categories.

Geographic range	Wide				Narrow			
Habitat specificity	Broad		Restricted		Broad		Restricted	
Abundance	Large	Small	Large	Small	Large	Small	Large	Small
Habitat occupancy high	9.5	0.9	5.0	7.7	7.3	0.0	8.2	35.5
9.4	1.0	7.3	11.5	8.3	0.0	12.5	28.1	
Habitat occupancy low	4.5	1.4	2.2	2.7	5.0	1.8	4.5	3.6
4.2	0.0	1.0	1.0	4.2	1.0	7.3	3.1	

There might be a problem, however, with using all of the species for this analysis. Species with habitat preferences outside of wet meadows (e.g., trees, xerophytes), would appear in this categorization as habitat specialists. Thus, we repeated the previous analysis using only those species classified as wet–grassland specialists or generalists. The overall pattern was similar, with a few exceptions. First, the endemic indicator species were more likely to have large than small abundances, although the total frequency of this category remained about the same. Second, there were increases in the frequency of species classified both as endangered and as indicators.

DISCUSSION

In general, there was a tendency for all species characteristics to be positively correlated. In other words, all possible combinations of traits shown in [Table 1B](#) were not found or were infrequent. Species tended either to have wide geographic ranges, broad habitat distributions, large local abundances, and high habitat occupancies or to have the opposite combination of traits. However, these were only general trends, and overall correlations were generally low to intermediate. For example, there were several species with restricted habitat distributions and large local abundances. These results suggest the existence of both superior species and specialists. A good example of a specialist is *Lysimachia vulgaris*. This species was found in just one plot, but in that plot it was by far the most abundant species.

As in a previous study of the British flora (Rabinowitz et al. 1986), we found little evidence for species with both broad habitat specificities and small abundances. The categories with the fewest species had either small mean abundances or low habitat occupancies. Such species will have the greatest vulnerability to demographic stochasticity (Lande 1988). Thus, such species may be infrequent because they tend to go extinct more often, rather than because they cannot evolve.

Conservation implications

Among the sampled species, none is officially listed as endangered in Iberia (Gómez–Campo 1987). However, three species (*Eleocharis quinqueflora*, *Ilex aquifolium*, and *Juncus bulbosus*) are included in the official catalog of endangered species of the Madrid regional government (CAM 1992). Our analysis classified the first two species as endemic indicators. Of the 28 plants within our endangered categories, *Cardamine pratensis*, *Carex panicea*, and *Juncus bulbosus* are actually rare species that could be considered as endangered in the studied region. Only one of them, however, is now officially considered vulnerable. Other species originally classified as endangered in our scheme were rare in wet grasslands only because they are woody species or species of other habitats such as xerophytes or mesophytes. Thus, an analysis such as ours is a useful first step in conservation efforts.

Tests of the theories

Support for the two theories was mixed, with evidence supporting and refuting both. Consider the predictions laid out in [Table 2](#). As predicted by the trade–off theory, the most frequent category was "endemic indicators." However, unlike the prediction for this theory, the "sparse" category had few species. As predicted by the superior organism category, the next most frequent categories were "common" and "endangered."

Geographic range, habitat specificity, and local abundance were all positively correlated in agreement with the superior organism theory, but not with the trade–off theory. On the other hand, the trade–off theory predicts the existence of species with very small volumes, high local abundance, and high occupancies. Such species were found in our samples (e.g., *Lysimachia vulgaris* and *Scirpus lacustris*).

With respect to the ecological groups, the predictions of neither theory were upheld with respect to local abundance and habitat occupancy (Tables 2 and 4). For environmental volume, the ordering of groups was consistent with the trade–off theory, although the differences were not statistically significant. Only for geographic range, based on distributions within Iberia, were the predictions upheld. Unfortunately, both theories make the same prediction, so these results fail to discriminate between them.

How general are our conclusions? Nearly all of the species in these plots were herbaceous. Trees and shrubs were nearly absent and always strays. Woody plants may differ in their patterns of commonness and rarity. In addition, we sampled only one habitat type, montane wet grasslands. On the other hand, patterns were generally strong across a large number of species and measures. For example, results concerning geographic ranges were consistent at both the regional and continental scales.

Evidence for the superior organism theory from other studies is mixed. A study of plant species distributions (Scheiner and Rey Benayas 1997) found a positive correlation between local abundance and habitat occupancy in 15 of 15 landscapes from across the globe. On the other hand, several reviews of animal species distributions (Gaston 1994, 1997, Lawton et al. 1994) found a positive correlation between geographic range and local abundance in only some studies, albeit the majority of them.

Speculations

An open question is how both superior species and habitat specialists can coexist. Superior species should outcompete specialists because of their greater habitat breadth. Why has this not occurred? It may be that the local populations of the superior species are not self–sustaining. They may be sink populations. This explanation is bolstered by the observation that the generalist species, which have the largest regional ranges, also have the lowest average local abundances ([Table 4](#)). These species may have superior dispersal abilities, creating the appearance of local dominance, whereas the specialists species are still able to outcompete them within their local niches. The mechanisms governing that competition are varied, including responses to herbivory, resource

fluctuation, and disturbance. Further, detailed studies are necessary to discover their workings.

We recognize that this explanation belongs to that class of ecological/evolutionary explanations of the sort "there has to be a trade-off somewhere." We (speaking collectively of ecologists and evolutionary biologists) regularly retreat to such explanations because we are otherwise unable to account for the persistence of diversity in the world. We recognize, though, that a "well it has to be there somewhere" defense is ultimately unsatisfactory. The resolution of this dilemma may lie in a close study of the apparently superior species to discover if and how we are being misled as to their nature. Three of those species (*Plantago lanceolata*, *P. major*, and *Trifolium repens*) are widespread weeds in North America. As such, they tend to be found in disturbed habitats, which is consistent with our "sink population" explanation.

Missing from either theory is an explanation of why a particular species is common or rare. Two recent reviews (Gaston 1994, Kunin 1997) list a number of causes of rarity. The proximal mechanisms reduce to three categories: ecological specialization, lack of dispersal, and historical contingency. Our data suggest that ecological specialization may be an important cause of rarity. Species with small environmental volumes tend to have lower abundances and, particularly, smaller geographic ranges. Whether this specialization is due to trade-offs or to being an inferior species is an open question. We speculate, however, that the answer is neither one nor the other. Both mechanisms probably play a role.

Further dissection of these categories is instructive (e.g., Rosenzweig and Lomolino 1997, and other chapters in Kunin and Gaston 1997) because they examine nonproximal mechanisms, those that cause ecological specialization. Among the suggested mechanisms are: breeding systems that favor selfing, low reproductive investment, low amounts of genetic variation, low population densities, and chaotic population dynamics. For animals, some of these syndromes are associated with larger body sizes (Gaston 1994).

In another analysis, Kelly (Kelly 1996, Kelly and Woodward 1996) searched for ecological correlates of commonness and rarity in the floras of Great Britain and Crete. She asked whether there are particular attributes of species that give them wide geographic ranges. Geographic range was defined similarly to our regional measure, the number of counties or 10 km² blocks in which a species appeared. She looked at a number of attributes, including life-form, pollination syndrome, and dispersal mechanism. Only life-form (trees were more common than shrubs) and pollination syndrome (wind-pollinated plants were more common than animal-pollinated plants) were found to explain geographic range. Unclear is the generality of these results. Both regions are islands. Will continental floras differ?

Our data do not address the dispersal issue. However, this mechanism implies that habitats contain less than the maximal number of species that they could hold. That is, if a species is rare only because it is unable to get to more suitable habitats, then other mechanisms such as competitive exclusion are not at work. Competitive exclusion would fall under the heading of rarity due to ecological specialization. Is there evidence for local areas with fewer species than might be expected based on factors such as levels of productivity? Yes. Two studies (Pärtel et al. 1996, Caley and Schluter 1997) found that local diversity was correlated with regional diversity. They (and we) interpret these results to suggest that local diversity is limited, in part, by the size of the regional species pool.

Thus, patterns of commonness and rarity appear to be linked with patterns of high and low diversity. These two aspects of species distributions are complementary and represent the patterns of column totals and row totals in a site-species matrix (e.g., [Appendix 1](#)). Typically, these two aspects of species distributions are studied separately. We suggest that integrating such studies will provide additional insights into both issues.

RESPONSES TO THIS ARTICLE

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APPENDICES

Appendix 1. Site-by-species data matrix showing the abundances of the 232 species in the 92 plots. Nomenclature follows Tutin et al. (1964, 1968, 1972, 1976, 1980).

A tab-delimited version of this appendix is available as a [text file](#).

	PLANTS	1	2	3	4	5	6
1	Achillea millefolium L.	0	0	0	0	0	0
2	Adenocarpus hispanicus (Lam.) DC.	0	0	0	0	0	0
3	Agrimonia eupatoria L.	0	0	0	0	0	0
4	Agrostis canina L.	0	0	0	0	0	0
5	Agrostis capillaris L.	0	0	0	0	0	0
6	Agrostis castellana Boiss. & Reuter	2	4	4	4	3	4
7	Agrostis stolonifera L.	0	0	0	0	0	0
8	Alchemilla filicaulis Buser	0	0	0	0	0	0
9	Alliaria petiolata (Bieb.) Cav. & Grand.	0	0	0	0	1	0
10	Allium oleraceum L.	0	0	0	0	0	0.1
11	Allium sphaerocephalon L.	0	0	0	0	0	0
12	Alnus glutinosa (L.) Gaertner	0	0	0	0	0	0
13	Alopecurus arundinaceus Poiret	0	0	0	0	0	0
14	Alopecurus geniculatus L.	0	0	0	0	0	0
15	Anagallis tenella (L.) L.	0	0	0	0	0	0
16	Anarrhinum bellidifolium (L.) Willd.	0	0	0	0.1	0	0
17	Anthoxanthum odoratum L.	0	0	0	0	0	0
18	Apium nodiflorum (L.) Lag.*	0	0	0	0	0	0
19	Aristolochia fontanesii Boiss. & Reut.	0	0	0	0	2	0
20	Arrhenatherum album (Vahl) W.D. Clayton	0	0	0	0.1	1	0
21	Arrhenatherum elatius (L.) Beauv. ex C. Presl.	0	0	0	0	0	0
22	Asphodelus ramosus L.	0	0	0	0	0	0
23	Baldellia ranunculoides (L.) Parl.	0	0	0	0	0	0
24	Bellis perennis L.	0	4	2	0	0.1	0
25	Betula pubescens Ehrh.	0	0	0	0	0	0
26	Brachypodium sylvaticum (Hudson) Beauv.	0	0	0	0	0	0
27	Briza media L.	0	0	0	0	0	0
28	Bryonia cretica L.	0	0	0	0	0.1	0
29	Calluna vulgaris (L.) Hull.	0	0	0	0	0	0
30	Campanula rapunculus L.	0	0	0	0	1	0
31	Cardamine pratensis L.	0	0	0	0	0	0
32	Carduncellus araneosus Boiss. & Reuter	0	0	0	0	0	0
33	Carduus carpetanus Boiss. & Reuter	0	0	0	0	0	0
34	Carex binervis Sm.	0	0	0	0	0	0
35	Carex demissa Hornem.	0	0	0	0	0	0
36	Carex divisa Hudson	0	3	2	2	0	0
37	Carex divulsa Stokes	0	0	0	1	1	0.1
38	Carex echinata Murray	0	0	0	0	0	0
39	Carex flacca Schreb.	0	0	0	0	0	0
40	Carex hirta L.	0	0	0	0	0	0
41	Carex muricata L. subsp. lamprocarpa Celak	0	0	0	1	0.1	0.1
42	Carex nigra (L.) Reich.	0	0	0	0	0	0
43	Carex ovalis Good.	0	0	0	0	0	0.1
44	Carex panicea L.	0	0	0	0	0	0
45	Carlina corymbosa L.	0	0.1	0.1	0	0	0
46	Carlina racemosa L.	0	0	0	0	0	0
47	Carum verticillatum (L.) Koch	0	0	0	0	0	0
48	Centaurea collina L.	0	0	0	0	0	0
49	Centaurea nigra L.	0	0	0	0	0	0
50	Centaurea scabiosa L.	0	0	0	0	0	0
51	Cerastium fontanum Baumg.	0	0	0	0	0	0
52	Chaerophyllum hirsutum L.	0	0	0	0	0	0
53	Chamaemelum nobile (L.) All.	0	2	2	0	0	0
54	Cirsium flavispina Boiss. ex DC.	0	0	0	0	0	0

55	Cirsium palustre (L.) Scop.	0	0	0	0	0	0
56	Clinopodium vulgare L.	0	0	0	0	0	0
57	Convolvulus arvensis L.	1	0	1	1	0	3
58	Corrigiola litoralis L.	0	0	0	0	0	0
59	Crataegus monogyna Jacq.	0	0	0	0	0	0
60	Crepis vesicaria L.	0	0	0	0	0	0
61	Cruciata glabra (L.) Ehr.	0	0	0	0	0	0
62	Cucubalus baccifer L.	0	0	0	0	0	0
63	Cynodon dactylon (L.) Pers.	0	4	3	4	0	1
64	Cynosurus cristatus L.	0	0.1	0.1	0	0	2
65	Cyperus longus L.	0	1	0	0	0	0
66	Cytisus purgans (L.) Boiss.	0	0	0	0	0	0
67	Dactylis glomerata L. subsp. (Roth) Nyman	0	0	0	0	0	0
68	Dactylorhiza elata(Poiter)Soó ssp.sesquipedalis(Willd.)Soó			1	0	0	0
69	Dactylorhiza sambucina (L.) Soó	0	0	0	0	0	0
70	Danthonia decumbens (L.) DC.	0	0	0	0	0	0
71	Daucus carota L.	0	0	0	0	0.1	0
72	Deschampsia refracta (Lag.) Roemer & Schultz	0	0	0	0	0	0
73	Dianthus deltoides L.	0	0	0	0	0	0
74	Dianthus scaber Chaix subsp. toletanus	0	0	0	0	0	0
75	Digitalis purpurea L.	0	0	0	0	0	0
76	Dipsacus fullonum L.	0	0	0	1	0	0
77	Eleocharis palustris (L.) Roem. & Schult.	0	0	0	0	0	0
78	Eleocharis quinqueflora (F.X.Hartm.) O.Schwarz	0	0	0	0	0	0
79	Eleocharis uniglumis (Link) Schultes	0	0	0	0	0	0
80	Elymus caninus (L.) L.	0	0	0	0	0	0
81	Epilobium hirsutum L.	0	0	0	0	0	0
82	Epilobium obscurum Schreber	0	0	0	0	0	0
83	Epilobium palustre L.	0	0	0	0	0	0
84	Equisetum palustre L.	0	0	0	0	0	0
85	Equisetum ramosissimum Desf.	0	0	0	0	0	0
86	Erica arborea L.	0	0	0	0	0	0
87	Erica tetralix L.	0	0	0	0	0	0
88	Eryngium campestre L.	0	0	0.1	0	0	0.1
89	Festuca ampla Hackel	0	0	0	0	0	0
90	Festuca arundinacea Schreber	0	0	0	0	0	0
91	Festuca costei (St.Yves) Markgr.-Dannemb.	0	0	0	0	0	0
92	Festuca iberica (Hackel) K. Richter	0	0	0	0	0	0
93	Festuca rothmaleri (Litard.) Markgr.-Dannemb.	0	0	0	3	1	3
94	Filipendula ulmaria (L.) Maxim.	0	0	0	0	0	0
95	Foeniculum vulgare Miller	0.1	0	0	0	0	0
96	Frangula alnus Miller	0	0	0	0	0	0
97	Fraxinus angustifolia Vahl	0	0	0	0	1	0
98	Galium palustre L.	0	0	0	0	0	0
99	Galium verum L.	0	0	0	0	0.1	0.1
100	Geum urbanum L.	0	0	0	0	0	0
101	Gladiolus illyricus Koch	0	0	0	0	0	0.1
102	Glyceria declinata Bréb.	0	0	0	0	0	0
103	Hedera helix L.	0	0	0	0	0.1	0
105	Heraclium sphondylium L.	0	0	0	0	0	0
106	Herniaria glabra L.	0	0	0	0	0	0
107	Hieracium pilosella L.	0	0	0	0	0	0
108	Holcus lanatus L.	0	0	0	0	0	0
109	Holcus mollis L.	0	0	0	0	0.1	0
110	Hordeum secalinum Schreb.	0	0	0	0	0	0
111	Hypericum humifusum L.	0	0	0	0	0	0
112	Hypericum undulatum Shous.ex Willd.	0	0	0	0	0	0
113	Hypochoeris radicata L.	0	1	1	1	0.1	2
114	Ilex aquifolium L.	0	0	0	0	0	0
116	Jasione montana L.	0	0	0	0	0	0
117	Juncus acutiflorus Ehrh. ex Hoffm.	0	0	0	0	0	0
118	Juncus articulatus L.	0	0	0	0	0	0
119	Juncus bulbosus L.	0	0	0	0	0	0
120	Juncus compressus Jacq.	0	0	0	0	0	0
121	Juncus effusus L.	0	0	0	0	0	0
122	Juncus heterophyllus Dufour	0	0	0	0	0	0

123	<i>Juncus inflexus</i> L.	0	0	0	0	0	0
124	<i>Juncus squarrosus</i> L.	0	0	0	0	0	4
125	<i>Juniperus communis</i> L. subsp. <i>nana</i> syme	0	0	0	0	0	0
126	<i>Knautia arvensis</i> (L.) Coulter (Briq.) Szabó	0	0	0	0	0	0
127	<i>Lavandula stoechas</i> L. subsp. <i>pedunculata</i> (Miller) Samp. ex Rozeira	0.1	0	0	0	0	0
128	<i>Leontodon carpetanus</i> Lange	0	0	0	0	0	0
129	<i>Leontodon tuberosus</i> L.	0	0	0	0	0	0
130	<i>Lepidium heterophyllum</i> Bentham	0	0	0	0	0	0
131	<i>Linum vienne</i> Miller	0	0	0	0	0	0
132	<i>Lolium perenne</i> L.	0	0	0	0	0.1	0
133	<i>Lonicera periclymenum</i> L.	0	0	0	0	0	0
134	<i>Lotus corniculatus</i> L.	0	0	0.1	0	0	1
135	<i>Luzula campestris</i> (L.) DC.	0	0	0	0	0	0
136	<i>Luzula forsteri</i> (Sm.) DC.	0	0	0	0	0	0
137	<i>Lychnis flos-cuculi</i> L.	0	0	0	0	0	0
138	<i>Lepidotis inundata</i> (L.) C. Börner	0	0	0	0	0	0
139	<i>Lycopus europaeus</i> L.	0	0	0	0	0	0
140	<i>Lygos sphaerocarpa</i> (L.) Heyw.	0.1	0	0	0	0	0
141	<i>Lysimachia vulgaris</i> L.	0	0	0	0	0	0
142	<i>Lythrum salicaria</i> L.	0	0	0	0	0	0
143	<i>Melica ciliata</i> L. ssp. <i>magnolii</i> (Gren.&Godron)Husnot	1	0	0	0	0	0
144	<i>Mentha cervina</i> L.	0	0	0	0	0	0
145	<i>Mentha pulegium</i> L.	0	1	0.1	0	0	0
146	<i>Mentha suaveolens</i> Ehrh.	0	0	1	1	0	0
147	<i>Merendera pyrenaica</i> (Pourret) P. Four.	0	0	0.1	0	0	0
148	<i>Molinia caerulea</i> (L.) Moench	0	0	0	0	0	0
149	<i>Myosotis stolonifera</i> (DC) Gay ex Leresche & Levier	0	0	0	0	0	0
151	<i>Narcissus bulbocodium</i> L.	0	0	0	0	0	0.1
152	<i>Nardus stricta</i> L.	0	0	0	0	0	0
153	<i>Nepeta nepetella</i> L.	0	0	0	0	0	0
154	<i>Oenanthe crocata</i> L.	0	0	0	0	0	0
155	<i>Ononis repens</i> L.	0	0	0	0.1	0	0
156	<i>Orchis coriophora</i> L. subsp. <i>fragrans</i> (Pollini) Sudre	0	0	0	0	0	0
157	<i>Oxalis acetosella</i> L.	0	0	0	0	0	0
158	<i>Parnassia palustris</i> L.	0	0	0	0	0	0
159	<i>Paronychia argentea</i> Lam.	0	0	0	0	0	0
160	<i>Pedicularis sylvatica</i> L.	0	0	0	0	0	0
161	<i>Peucedanum officinale</i> L.	0	0	0	0	0	0
162	<i>Phleum pratense</i> L. subsp. <i>bertoloni</i> (DC.) Bornm.	0	0	0	0	0	0
163	<i>Pinus sylvestris</i> L.	0	0	0	0	0	0
164	<i>Plantago alpina</i> L. subsp. <i>penyalarensis</i> (Pau) Rivas Martinez	0	0	0	0	0	0
165	<i>Plantago coronopus</i> L.	0	0.1	0	0	0	0
166	<i>Plantago lanceolata</i> L.	1	1	1	1	1	1
167	<i>Plantago major</i> L.	0	0	0	0	0	0
168	<i>Poa bulbosa</i> L.	0.1	0	0	0	0	0
169	<i>Poa trivialis</i> L.	0	0	0	0	0	0
170	<i>Polygala vulgaris</i> L.	0	0	0	0	0	0
171	<i>Polygonum bistorta</i> L.	0	0	0	0	0	0
172	<i>Potamogeton perfoliatus</i> L.	0	0	0	0	0	0
173	<i>Potentilla erecta</i> (L.) Räuschel	0	0	0	0	0	0
174	<i>Potentilla hirta</i> L.	0	0	0	0	1	0
175	<i>Potentilla reptans</i> L.	0	0	0	2	0	0
176	<i>Prunella grandiflora</i> (L.) Scholler	0	0	0	0	0	0
177	<i>Prunella laciniata</i> (L.) L.	0	0	0	0	0	0
178	<i>Prunella vulgaris</i> L.	0	0	0	0	0	0
179	<i>Prunus spinosa</i> L.	0	0	0	0	3	0
180	<i>Pteridium aquilinum</i> (L.) Kuhn.	0	0	0	0	0	0
181	<i>Quercus pyrenaica</i> Willd.	0	0	0	0	0.1	0
182	<i>Quercus ilex</i> L. subsp. <i>rotundifolia</i> (Lam.) Tab. Morais	0.1	0	0	0	0	0
183	<i>Ranunculus acris</i> L.	0	0	0	0	0	0
184	<i>Ranunculus bulbosus</i> L.	0	1	0.1	1	0	1
185	<i>Ranunculus flammula</i> L.	0	0	0	0	0	0
186	<i>Ranunculus paludosus</i> Desf.	0	0	0	1	0	0
187	<i>Ranunculus repens</i> L.	0	0	0	0	0	0
188	<i>Rhamnus cathartica</i> L.	0	0	0	0	0	0
189	<i>Rhinanthus minor</i> L.	0	0	0	0	0	0

191	Rubus ulmifolius Schott	0	0	0	0	2	0
192	Rumex acetosella L.	0	0	0	0	0	0
194	Rumex conglomeratus Murray	0	0	0	0	0	0
195	Rumex crispus L.	0	0	0	0	0	0
196	Rumex papillaris Boiss. & Reuter	0.1	0	0	1	1	1
197	Rumex pulcher L.	1	0	0.1	0	0.1	0
198	Sagina nevadensis Boiss. & Reuter	0	0	0	0	0	0
199	Salix atrocinerea Brot.	0	0	0	0	0	0
200	Sanguisorba minor Scop. subsp. minor	2	0	0	1	0	0
201	Sanguisorba officinalis L.	0	0	0	0	0	0
202	Santolina rosmarinifolia L.	0	0	0	0	0	0
203	Scirpus holoschoenus L.	3	0	3	0	0	0
204	Scirpus lacustris L.	0	0	0	0	0	0
205	Scirpus setaceus L.	0	0	0	0	0	0
206	Scolymus hispanicus L.	1	0	0	0	0	0
207	Scrophularia auriculata L.	0	0	0	0	0	0
208	Senecio jacobaea L.	1	0	0	1	1	0.1
209	Silene vulgaris (Moench) Garcke	0	0	0	0	0.1	0
210	Sisymbrella aspera (L.) Spach	0	0	0	0	0	0
211	Spiranthes aestivalis (Poirot) L.C.M. Richard	0	0	0	0	0	0
212	Stellaria graminea L.	0	0	0	0	0	0
213	Succisa pratensis Moench	0	0	0	0	0	0
214	Tamus communis L.	0	0	0	0	1	0
215	Taraxacum officinale group.	0	0	0	0	0.1	0
216	Teucrium scorodonia L.	0	0	0	0	0	0
217	Thapsia villosa L.	0	0	0	0	0	0
218	Trifolium fragiferum L.	0	1	0	0	0	0
219	Trifolium pratense L.	0	0	0	0	1	0
220	Trifolium repens L.	0	0	0	0	0.1	0
221	Trisetum flavescens (L.) Beauv.	0	0	0	0	0	0
222	Urtica dioica L.	0	0	0	0	0	0
223	Valeriana officinalis L.	0	0	0	0	0	0
224	Verbascum sinuatum L.	0	0	0	0	0.1	0
225	Verbena officinalis L.	0	0	0	1	0	0
226	Veronica anagallis-aquatica L.	0	0	0	0	0	0
227	Veronica catenata Pennell	0	0	0	0	0	0
228	Veronica beccabunga L.	0	0	0	0	0	0
229	Veronica officinalis L.	0	0	0	0	0	0
230	Veronica scutellata L.	0	0	0	0	0	0
231	Veronica serpyllifolia L.	0	0	0	0	0	0
232	Viburnum opulus L.	0	0	0	0	0	0
233	Viola canina L.	0	0	0	0	0	0
234	Viola odorata L.	0	0	0	0	0	0
235	Viola palustris L. subsp. Juressi (Link ex K. Wein) Coutinho	0	0	0	0	0	0
236	Viola riviniana Reichenb.	0	0	0	0	0	0
237	Wahlenbergia hederacea (L.) Reich.	0	0	0	0	0	0

Appendix 2. Ecological information for the 232 species. Abbreviations: A1, Axis 1, etc.; min., minimum; max., maximum; len., length; env. vol., environmental volume; Sites, no. sites found; ab., abundance; Occ., habitat occupancy; Grp., habitat group; Eur., European range; N. Afr., North African range; Cont., continental range; Iber. (km²), Iberian range.

A tab-delimited version of this appendix is available as a [text file](#).

Plant	A1 max	A1 min	A2 max	A2 min	A3 max	A3 min	A1 len.	A2 len.	A3 len.	Envir. vol.	Sites
1	0.1645	0.0806	0.1733	0.1301	0.0029	-0.0587	0.0839	0.0432	0.0616	0.0005325160	2
2	0.2037	0.0044	0.1602	0.1094	0.1070	-0.1120	0.1993	0.0508	0.2190	0.0052883640	2
3	-0.0813	-0.0813	0.0143	0.0143	-0.0425	-0.0425	0.0000	0.0000	0.0000	0.0000000000	1
4	0.4230	-0.1432	0.1878	-0.4377	0.2484	-0.1797	0.5662	0.6255	0.4281	0.3616168164	32
5	0.0044	0.0044	0.1602	0.1602	0.1070	0.1070	0.0000	0.0000	0.0000	0.0000000000	1
6	0.2632	-0.3533	0.3545	-0.4377	0.2224	-0.3766	0.6165	0.7922	0.5990	0.6977517798	62
7	0.2037	-0.4238	0.1878	-0.1812	0.1041	-0.1797	0.6275	0.3690	0.2838	0.1567323694	12
8	0.0806	0.0395	0.1301	0.1106	0.0444	0.0029	0.0411	0.0195	0.0415	0.0000793288	2

9	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
10	-0.3396	-0.3526	-0.0592	-0.0961	0.0883	0.0704	0.0130	0.0369	0.0179	0.0000204800	2
11	-0.2724	-0.2992	-0.2719	-0.3640	-0.3119	-0.3766	0.0268	0.0921	0.0647	0.0003808947	2
12	0.0855	0.0855	0.1873	0.1873	-0.0596	-0.0596	0.0000	0.0000	0.0000	0.0000000000	1
13	0.2101	-0.3533	0.2071	-0.1800	0.2181	-0.2050	0.5634	0.3871	0.4231	0.2200843953	10
14	-0.2659	-0.3323	-0.0229	-0.0579	0.2181	0.1041	0.0664	0.0350	0.1140	0.0006318983	2
15	0.2377	0.0450	0.0869	-0.1812	-0.0372	-0.1797	0.1927	0.2681	0.1425	0.0175589930	7
16	-0.2843	-0.2843	0.0401	0.0401	-0.0682	-0.0682	0.0000	0.0000	0.0000	0.0000000000	1
17	0.4230	-0.1432	0.2415	-0.1881	0.2224	-0.1797	0.5662	0.4296	0.4021	0.2332783433	33
18	0.2037	-0.1432	0.1094	-0.1812	0.0062	-0.1797	0.3469	0.2906	0.1859	0.0446977345	4
19	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
20	0.0395	-0.2885	0.1106	0.0221	0.0444	-0.1832	0.3280	0.0885	0.2276	0.0157578000	5
21	0.0044	0.0044	0.1602	0.1602	0.1070	0.1070	0.0000	0.0000	0.0000	0.0000000000	1
22	-0.0615	-0.3387	0.3545	0.0531	0.1412	-0.0643	0.2772	0.3014	0.2055	0.0409500571	3
23	-0.0955	-0.0955	-0.0792	-0.0792	-0.0060	-0.0060	0.0000	0.0000	0.0000	0.0000000000	1
24	0.2283	-0.2885	0.3545	-0.1800	0.0333	-0.2050	0.5168	0.5345	0.2383	0.1570002950	14
25	0.2130	-0.1432	0.2105	0.1086	0.1452	-0.1115	0.3562	0.1019	0.2567	0.0222228717	5
26	0.1574	-0.2247	0.1873	-0.1361	-0.0425	-0.1758	0.3821	0.3234	0.1333	0.0392874114	5
27	0.2377	-0.1432	0.1602	-0.4377	0.2224	-0.1797	0.3809	0.5979	0.4021	0.2184136672	21
28	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
29	0.2757	-0.0813	0.1438	-0.1036	0.0662	-0.0425	0.3570	0.2474	0.1087	0.0228983225	3
30	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
31	0.2130	0.0278	0.2105	-0.0330	0.1452	-0.1115	0.1852	0.2435	0.2567	0.0276103574	3
32	-0.4238	-0.4238	-0.0139	-0.0139	0.0626	0.0626	0.0000	0.0000	0.0000	0.0000000000	1
33	0.2632	-0.1964	0.2415	-0.0501	0.0441	-0.1132	0.4596	0.2916	0.1573	0.0502808341	4
34	0.3388	-0.2593	0.2415	-0.4377	0.2224	-0.1832	0.5981	0.6792	0.4056	0.3929846956	36
35	0.4230	0.0450	0.1733	-0.2314	0.1976	-0.1797	0.3780	0.4047	0.3773	0.1376632508	25
36	-0.1722	-0.3924	0.2071	-0.3640	0.1324	-0.3766	0.2202	0.5711	0.5090	0.1526699167	12
37	0.2127	-0.3396	0.0514	-0.0592	0.0704	-0.1132	0.5523	0.1106	0.1836	0.0267490929	4
38	0.4230	0.0278	0.2415	-0.2314	0.2484	-0.1797	0.3952	0.4729	0.4281	0.1908260626	24
39	0.2283	-0.0813	0.1301	-0.4377	0.1503	-0.1727	0.3096	0.5678	0.3230	0.1354269426	10
40	0.1574	-0.3087	0.1878	-0.1361	0.1463	-0.1758	0.4661	0.3239	0.3221	0.1159810369	9
41	0.0214	-0.4238	0.0686	-0.1361	0.1463	-0.0916	0.4452	0.2047	0.2379	0.0517098945	9
42	0.4230	0.0746	0.1321	-0.2314	0.2484	-0.1797	0.3484	0.3635	0.4281	0.1293105625	20
43	0.3388	-0.3533	0.2415	-0.4377	0.2224	-0.1779	0.6921	0.6792	0.4003	0.4488056629	37
44	0.2757	0.0044	0.1602	-0.2438	0.2224	-0.1797	0.2713	0.4040	0.4021	0.1051166335	12
45	-0.2308	-0.2314	-0.0740	-0.1706	-0.0628	-0.1177	0.0006	0.0966	0.0549	0.0000075894	2
46	-0.2362	-0.2838	0.2423	0.0593	0.0702	-0.0049	0.0476	0.1830	0.0751	0.0015602859	2
47	0.4230	-0.3533	0.2415	-0.4377	0.2224	-0.3766	0.7763	0.6792	0.5990	0.7532866960	51
48	-0.1727	-0.1727	0.3545	-0.3545	-0.0643	-0.0643	0.0000	0.0000	0.0000	0.0000000000	1
49	0.0249	-0.1864	0.1878	0.0143	0.0583	-0.1779	0.2113	0.1735	0.2362	0.0206530921	4
50	-0.4238	-0.4238	-0.0139	-0.0139	0.0626	0.0626	0.0000	0.0000	0.0000	0.0000000000	1
51	0.3395	-0.2247	0.2415	-0.1361	0.1278	-0.1388	0.5642	0.3776	0.2666	0.1354663483	21
52	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
53	0.1300	-0.3533	0.0834	-0.1706	0.0187	-0.1727	0.4833	0.2540	0.1914	0.0560400684	9
54	0.2127	-0.4238	0.1086	-0.1361	0.0626	-0.1132	0.6365	0.2447	0.1758	0.0653066580	4
55	0.2283	0.2130	0.2105	0.0636	-0.1084	-0.1115	0.0153	0.1469	0.0031	0.0000166181	2
56	0.1439	-0.0813	0.0143	0.0023	-0.0425	-0.1758	0.2252	0.0120	0.1333	0.0008591836	2
57	-0.0244	-0.3396	0.2423	-0.1706	0.1412	-0.1247	0.3152	0.4129	0.2659	0.0825383230	12
58	-0.0818	-0.0818	-0.0733	-0.0733	-0.0647	-0.0647	0.0000	0.0000	0.0000	0.0000000000	1
59	0.0958	-0.2659	0.1086	-0.1800	0.1041	-0.2050	0.3617	0.2886	0.3091	0.0769573407	6
60	-0.3387	-0.3387	0.0733	0.0733	0.1412	0.1412	0.0000	0.0000	0.0000	0.0000000000	1
61	0.3395	0.1651	0.1321	0.0536	0.1278	-0.0284	0.1744	0.0785	0.1562	0.0051003899	3
62	0.0249	-0.2247	0.1878	-0.1361	-0.0477	-0.0690	0.2496	0.3239	0.0213	0.0041071574	2
63	-0.0818	-0.4238	0.2423	-0.3640	0.1463	-0.3766	0.3420	0.6063	0.5229	0.2586059588	15
64	0.2632	-0.4238	0.2423	-0.4377	0.2181	-0.3766	0.6870	0.6800	0.5947	0.6626280249	55
65	0.2037	-0.4238	0.2423	-0.1361	0.0702	-0.1120	0.6275	0.3784	0.1822	0.1031856827	9
66	0.1645	0.1645	0.1733	0.1733	-0.0587	-0.0587	0.0000	0.0000	0.0000	0.0000000000	1
67	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
68	0.1439	-0.2885	0.2423	-0.1800	0.1070	-0.2050	0.4324	0.4223	0.3120	0.1358837652	9
69	0.0806	-0.1864	0.1602	0.1009	0.1070	-0.1779	0.2670	0.0593	0.2849	0.0107588194	3
70	0.2377	-0.3087	0.2071	-0.4377	0.2224	-0.1779	0.5464	0.6448	0.4003	0.3363779512	31
71	-0.0615	-0.4238	0.0531	-0.1800	0.0883	-0.2050	0.3623	0.2331	0.2933	0.0590784214	6
72	0.2101	-0.3533	0.1602	-0.4377	0.2224	-0.1779	0.5634	0.5979	0.4003	0.3216156678	15
73	-0.0615	-0.0615	0.0531	0.0531	0.0583	0.0583	0.0000	0.0000	0.0000	0.0000000000	1
74	0.2101	0.2101	0.1602	0.1602	-0.0017	-0.0017	0.0000	0.0000	0.0000	0.0000000000	1

75	0.2632	0.2632	0.2415	0.2415	-0.0092	-0.0092	0.0000	0.0000	0.0000	0.0000000000	1
76	-0.2843	-0.2843	0.0401	0.0401	-0.0682	-0.0682	0.0000	0.0000	0.0000	0.0000000000	1
77	0.2377	-0.3544	0.1878	-0.1487	0.1870	-0.1577	0.5921	0.3365	0.3447	0.1638051775	13
78	0.2757	0.1302	0.0174	-0.1036	0.0525	-0.0517	0.1455	0.1210	0.1042	0.0043754457	3
79	0.0450	0.0450	0.0029	0.0029	-0.0410	-0.0410	0.0000	0.0000	0.0000	0.0000000000	1
80	0.1574	-0.0813	0.0961	0.0143	-0.0425	-0.1717	0.2387	0.0818	0.1292	0.0060169229	2
81	0.1773	-0.1432	0.1086	0.0348	0.0620	0.0062	0.3205	0.0738	0.0558	0.0031479281	2
82	0.4230	-0.1432	0.2105	-0.2314	0.2224	-0.1132	0.5662	0.4419	0.3356	0.2002728279	21
83	0.2101	0.1685	0.1602	-0.1236	0.0894	-0.0017	0.0416	0.2838	0.0911	0.0025652536	2
84	-0.1432	-0.1432	0.1086	0.1086	0.0062	0.0062	0.0000	0.0000	0.0000	0.0000000000	1
85	-0.0813	-0.0813	0.0143	0.0143	-0.0425	-0.0425	0.0000	0.0000	0.0000	0.0000000000	1
86	0.2130	-0.0813	0.2105	0.0143	0.1452	-0.1115	0.2943	0.1962	0.2567	0.0353525989	4
87	0.3305	0.3305	-0.0456	-0.0456	0.1578	0.1578	0.0000	0.0000	0.0000	0.0000000000	1
88	0.2037	-0.3526	0.3545	-0.1706	0.1412	-0.1727	0.5563	0.5251	0.3139	0.2186999106	15
89	0.1574	-0.2838	0.2423	0.0961	0.0702	-0.1717	0.4412	0.1462	0.2419	0.0372155941	2
90	-0.1722	-0.2992	0.1009	-0.3640	-0.1779	-0.3766	0.1270	0.4649	0.1987	0.0279812651	4
91	0.2236	0.1302	0.1255	-0.0531	-0.0419	-0.1577	0.0934	0.1786	0.1158	0.0046072640	4
92	0.4230	0.0044	0.2415	-0.4377	0.2484	-0.1132	0.4186	0.6792	0.3616	0.2452062494	28
93	0.2037	-0.3526	0.3545	-0.3640	0.1463	-0.3766	0.5563	0.7185	0.5229	0.4984948613	35
94	0.0806	-0.1432	0.1301	0.1086	0.0062	0.0029	0.2238	0.0215	0.0033	0.0000378720	2
95	-0.2362	-0.2362	0.0186	0.0186	-0.1247	-0.1247	0.0000	0.0000	0.0000	0.0000000000	1
96	0.1651	-0.0813	0.1602	0.0143	0.1452	-0.0425	0.2464	0.1459	0.1877	0.0160940920	4
97	0.0855	-0.3323	0.1873	-0.1800	0.2181	-0.2050	0.4178	0.3673	0.4231	0.1548597668	11
98	0.3395	-0.1432	0.2415	-0.4377	0.2224	-0.1717	0.4827	0.6792	0.3941	0.3081680586	29
99	0.2101	-0.3396	0.1838	-0.0945	0.1463	-0.1758	0.5497	0.2783	0.3221	0.1175265208	21
100	0.1579	-0.2247	0.1086	-0.1881	0.2224	-0.0690	0.3826	0.2967	0.2914	0.0788965969	4
101	-0.3396	-0.3396	-0.0592	-0.0592	0.0704	0.0704	0.0000	0.0000	0.0000	0.0000000000	1
102	0.3305	-0.3323	0.2415	-0.2438	0.2224	-0.2050	0.6628	0.4853	0.4274	0.3278940382	31
103	-0.1432	-0.2885	0.1086	0.0514	0.0333	0.0062	0.1453	0.0572	0.0271	0.0005372014	2
105	0.0806	0.0806	0.1301	0.1301	0.0029	0.0029	0.0000	0.0000	0.0000	0.0000000000	1
106	0.0452	-0.0818	0.0608	-0.1487	0.0187	-0.0709	0.1270	0.2095	0.0896	0.0056859360	3
107	0.3395	-0.2992	0.3545	-0.3640	0.2224	-0.3766	0.6387	0.7185	0.5990	0.6556268372	25
108	0.2632	-0.4238	0.2423	-0.4377	0.2224	-0.1797	0.6870	0.6800	0.4021	0.4480288024	41
109	0.2130	-0.3087	0.2105	-0.0229	0.1463	-0.1832	0.5217	0.2334	0.3295	0.0956936938	7
110	-0.0965	-0.2724	-0.1800	-0.2719	-0.2050	-0.3119	0.1759	0.0919	0.1069	0.0041215946	2
111	0.0214	0.0214	-0.0047	-0.0047	-0.0916	-0.0916	0.0000	0.0000	0.0000	0.0000000000	1
112	0.2632	-0.1722	0.2415	-0.1881	0.2224	-0.1832	0.4354	0.4296	0.4056	0.1809492783	16
113	0.2632	-0.3533	0.3545	-0.3640	0.2224	-0.3766	0.6165	0.7185	0.5990	0.6328384925	43
114	0.0278	0.0278	0.1327	0.1327	0.1452	0.1452	0.0000	0.0000	0.0000	0.0000000000	1
116	0.2037	-0.2838	0.3545	0.0585	0.0702	-0.1120	0.4875	0.2960	0.1822	0.0627077063	4
117	0.4230	-0.3533	0.2415	-0.3640	0.2224	-0.3766	0.7763	0.6055	0.5990	0.6715475478	50
118	0.4230	0.1251	0.1602	-0.2314	0.2224	-0.1797	0.2979	0.3916	0.4021	0.1118802610	19
119	0.4230	0.0278	0.2105	-0.0788	0.1950	-0.1115	0.3952	0.2893	0.3065	0.0835799409	7
120	-0.4238	-0.4238	-0.0139	-0.0139	0.0626	0.0626	0.0000	0.0000	0.0000	0.0000000000	1
121	0.3395	-0.3087	0.2415	-0.4377	0.2224	-0.1832	0.6482	0.6792	0.4056	0.4259031595	38
122	0.0790	0.0790	-0.0651	-0.0651	0.1557	0.1557	0.0000	0.0000	0.0000	0.0000000000	1
123	-0.1964	-0.3323	0.0221	-0.0579	0.2181	0.0441	0.1359	0.0800	0.1740	0.0045119565	2
124	0.4230	-0.3396	0.2071	-0.4377	0.2484	-0.1779	0.7626	0.6448	0.4263	0.4999693415	28
125	0.4230	-0.0813	0.1438	-0.1848	0.2484	-0.0675	0.5043	0.3286	0.3159	0.1248568473	14
126	0.0806	0.0806	0.1301	0.1301	0.0029	0.0029	0.0000	0.0000	0.0000	0.0000000000	1
127	0.0044	-0.2838	0.2423	0.0186	0.1070	-0.1247	0.2882	0.2237	0.2317	0.0356280625	3
128	0.2377	-0.3533	0.1838	-0.1881	0.2224	-0.1797	0.5910	0.3719	0.4021	0.2107919123	18
129	-0.0813	-0.0813	0.0143	0.0143	-0.0425	-0.0425	0.0000	0.0000	0.0000	0.0000000000	1
130	0.2127	-0.2247	0.0608	-0.1361	-0.0647	-0.1727	0.4374	0.1969	0.1080	0.0221847461	8
131	-0.1999	-0.1999	0.0825	0.0825	0.0232	0.0232	0.0000	0.0000	0.0000	0.0000000000	1
132	0.2236	-0.4238	0.0834	-0.3640	0.1041	-0.3766	0.6474	0.4474	0.4807	0.3320848082	14
133	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
134	0.4230	-0.4238	0.2423	-0.4377	0.2224	-0.1832	0.8468	0.6800	0.4056	0.5570496682	58
135	0.3395	-0.1432	0.2415	-0.4377	0.2224	-0.1758	0.4827	0.6792	0.3982	0.3113740699	18
136	0.2127	0.0855	0.1873	-0.0501	-0.0596	-0.1132	0.1272	0.2374	0.0536	0.0038604580	2
137	0.1773	-0.1432	0.1086	0.0348	0.0620	0.0062	0.3205	0.0738	0.0558	0.0031479281	2
138	0.3094	0.3094	-0.0788	-0.0788	0.1950	0.1950	0.0000	0.0000	0.0000	0.0000000000	1
139	0.0249	0.0249	0.1878	0.1878	-0.0477	-0.0477	0.0000	0.0000	0.0000	0.0000000000	1
140	-0.2362	-0.2362	0.0186	0.0186	-0.1247	-0.1247	0.0000	0.0000	0.0000	0.0000000000	1
141	0.0855	0.0855	0.1873	0.1873	-0.0596	-0.0596	0.0000	0.0000	0.0000	0.0000000000	1
142	-0.1864	-0.1864	0.1009	0.1009	-0.1779	-0.1779	0.0000	0.0000	0.0000	0.0000000000	1

143	-0.2362	-0.2362	0.0186	0.0186	-0.1247	-0.1247	0.0000	0.0000	0.0000	0.0000000000	1
144	0.0790	-0.3924	0.0560	-0.0651	0.1557	0.1324	0.4714	0.1211	0.0233	0.0031724578	2
145	0.2377	-0.3533	0.3545	-0.2719	0.2224	-0.3119	0.5910	0.6264	0.5343	0.4717703206	34
146	0.2632	-0.4238	0.2415	-0.1706	0.0626	-0.1758	0.6870	0.4121	0.2384	0.1609799596	13
147	0.3395	-0.2724	0.1838	-0.2719	0.1278	-0.3119	0.6119	0.4557	0.4397	0.2924301580	10
148	0.0249	0.0249	0.1878	0.1878	-0.0477	-0.0477	0.0000	0.0000	0.0000	0.0000000000	1
149	0.4230	0.0278	0.2415	-0.4377	0.2484	-0.1797	0.3952	0.6792	0.4281	0.2740728731	28
151										0.3921523124	7
152	0.4230	-0.3087	0.2071	-0.4377	0.2484	-0.1758	0.7317	0.6448	0.4242	0.4773478376	49
153	-0.0813	-0.0813	0.0143	0.0143	-0.0425	-0.0425	0.0000	0.0000	0.0000	0.0000000000	1
154	0.0249	-0.0965	0.1878	-0.1800	-0.0477	-0.2050	0.1214	0.3678	0.1573	0.0167519491	2
155	-0.2838	-0.2843	0.2423	0.0401	0.0702	-0.0682	0.0005	0.2022	0.1384	0.0000333729	2
156	0.0746	-0.3396	0.0534	-0.0592	0.0704	0.0464	0.4142	0.1126	0.0240	0.0026697214	3
157	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
158	0.4230	0.2947	0.0714	-0.2314	0.1976	0.0501	0.1283	0.3028	0.1475	0.0136672381	4
159	0.0214	0.0214	-0.0047	-0.0047	-0.0916	-0.0916	0.0000	0.0000	0.0000	0.0000000000	1
160	0.4230	-0.0813	0.2415	-0.1812	0.1278	-0.1797	0.5043	0.4227	0.3075	0.1563408784	14
161	-0.2724	-0.2724	-0.2719	-0.2719	-0.3119	-0.3119	0.0000	0.0000	0.0000	0.0000000000	1
162	-0.0615	-0.3533	0.0834	-0.3640	0.2181	-0.3766	0.2918	0.4474	0.5947	0.1851763064	7
163	0.2377	-0.0197	0.2105	-0.2438	0.2224	-0.1132	0.2574	0.4543	0.3356	0.0936007747	9
164	0.2588	0.2588	-0.1848	-0.1848	0.2484	0.2484	0.0000	0.0000	0.0000	0.0000000000	1
165	0.1300	-0.2362	0.3545	-0.1800	0.0573	-0.2050	0.3662	0.5345	0.2623	0.1224533164	7
166	0.2127	-0.4238	0.3545	-0.3640	0.1412	-0.3766	0.6365	0.7185	0.5178	0.5647983744	34
167	0.2236	-0.4238	0.1838	-0.0441	0.0626	-0.1577	0.6474	0.2279	0.2203	0.0775242778	6
168	-0.2362	-0.2362	0.0186	0.0186	-0.1247	-0.1247	0.0000	0.0000	0.0000	0.0000000000	1
169	0.2632	-0.4238	0.2415	-0.4377	0.1503	-0.3766	0.6870	0.6792	0.5269	0.5863930636	42
170	0.1574	-0.0813	0.1301	0.0143	0.0029	-0.1717	0.2387	0.1158	0.1746	0.0115109569	3
171	0.0806	-0.1432	0.1301	0.1086	0.0444	0.0029	0.2238	0.0215	0.0415	0.0004762696	3
172	0.2377	0.1302	0.0869	-0.0531	-0.0419	-0.0481	0.1075	0.1400	0.0062	0.0002225535	2
173	0.4230	-0.1432	0.1602	-0.2314	0.2224	-0.1758	0.5662	0.3916	0.3982	0.2105814033	23
174	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
175	0.1447	-0.2843	0.0401	-0.2438	0.0446	-0.0682	0.4290	0.2839	0.1128	0.0327670992	2
176	0.0806	0.0806	0.1301	0.1301	0.0029	0.0029	0.0000	0.0000	0.0000	0.0000000000	1
177	0.2037	-0.3387	0.3545	0.0593	0.1412	-0.1717	0.5424	0.2952	0.3129	0.1194944704	6
178	0.3388	-0.3087	0.2415	-0.4377	0.2224	-0.1832	0.6475	0.6792	0.4056	0.4254432208	42
179	-0.0813	-0.2885	0.1086	0.0143	0.0333	-0.0425	0.2072	0.0943	0.0758	0.0035324568	3
180	0.2130	-0.0813	0.2105	-0.0501	0.1452	-0.1758	0.2943	0.2606	0.3210	0.0587186304	6
181	0.0855	-0.2885	0.1873	-0.1800	0.0583	-0.2050	0.3740	0.3673	0.2633	0.0862679745	5
182	-0.2362	-0.2362	0.0186	0.0186	-0.1247	-0.1247	0.0000	0.0000	0.0000	0.0000000000	1
183	0.0806	0.0395	0.1301	0.1106	0.0444	0.0029	0.0411	0.0195	0.0415	0.0000793288	2
184	0.4230	-0.3533	0.2415	-0.4377	0.2224	-0.3766	0.7763	0.6792	0.5990	0.7532866960	48
185	0.4230	-0.2659	0.2415	-0.1881	0.2224	-0.1832	0.6889	0.4296	0.4056	0.2863021539	20
186	-0.0818	-0.2843	0.0401	-0.0733	-0.0647	-0.0682	0.2025	0.1134	0.0035	0.0001916957	2
187	0.2632	-0.2098	0.2415	-0.1288	0.1452	-0.1832	0.4730	0.3703	0.3284	0.1371905549	23
188	0.2130	-0.0965	0.2105	-0.1800	-0.1115	-0.2050	0.3095	0.3905	0.0935	0.0269525285	2
189	0.0395	0.0395	0.1106	0.1106	0.0444	0.0444	0.0000	0.0000	0.0000	0.0000000000	1
191	0.2632	-0.2885	0.2415	-0.1361	0.1452	-0.1120	0.5517	0.3776	0.2572	0.1277944948	13
192	0.2283	-0.3526	0.3545	-0.1361	0.0883	-0.1727	0.5809	0.4906	0.2610	0.1774089964	16
194	0.0395	-0.3533	0.1106	-0.1800	0.1041	-0.2050	0.3928	0.2906	0.3091	0.0841535237	7
195	-0.0197	-0.3924	0.0560	-0.1800	0.2181	-0.2050	0.3727	0.2360	0.4231	0.0887606824	6
196	0.0806	-0.3526	0.2423	-0.1361	0.1412	-0.1247	0.4332	0.3784	0.2659	0.1039594862	15
197	-0.2308	-0.2885	0.0514	-0.1706	0.0333	-0.1247	0.0577	0.2220	0.1580	0.0048271644	3
198	0.3348	0.3348	-0.0166	-0.0166	0.0564	0.0564	0.0000	0.0000	0.0000	0.0000000000	1
199	0.2632	-0.1722	0.2415	0.0143	0.1070	-0.1832	0.4354	0.2272	0.2902	0.0684700069	7
200	0.0452	-0.2843	0.1106	-0.1800	0.0444	-0.2050	0.3295	0.2906	0.2494	0.0569578634	7
201	0.1447	0.1447	-0.2438	-0.2438	0.0446	0.0446	0.0000	0.0000	0.0000	0.0000000000	1
202	0.0455	0.0452	0.0608	-0.0108	-0.0709	-0.0822	0.0003	0.0716	0.0113	0.0000005789	2
203	-0.2308	-0.4238	0.2423	-0.1706	0.1463	-0.1247	0.1930	0.4129	0.2710	0.0515083567	5
204	-0.1845	-0.1845	-0.1419	-0.1419	0.1870	0.1870	0.0000	0.0000	0.0000	0.0000000000	2
205	0.2632	-0.3533	0.2415	-0.1812	0.0573	-0.1797	0.6165	0.4227	0.2370	0.1473058133	14
206	-0.2362	-0.4238	0.0186	-0.0961	0.0883	-0.1247	0.1876	0.1147	0.2130	0.0109315581	3
207	-0.1432	-0.1432	0.1086	0.1086	0.0062	0.0062	0.0000	0.0000	0.0000	0.0000000000	1
208	0.2632	-0.4238	0.3545	-0.3640	0.1463	-0.3766	0.6870	0.7185	0.5229	0.6156138230	38
209	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
210	0.1773	-0.0244	0.0348	-0.1487	0.0620	0.0187	0.2017	0.1835	0.0433	0.0038223995	2
211	0.1496	0.1496	0.0078	0.0078	-0.1388	-0.1388	0.0000	0.0000	0.0000	0.0000000000	1

212	0.0395	0.0395	0.1106	0.1106	0.0444	0.0444	0.0000	0.0000	0.0000	0.0000000000	1
213	0.0806	0.0395	0.1301	0.1106	0.0444	0.0029	0.0411	0.0195	0.0415	0.0000793288	2
214	-0.2885	-0.2885	0.0514	0.0514	0.0333	0.0333	0.0000	0.0000	0.0000	0.0000000000	1
215	0.2632	-0.2885	0.2415	-0.2438	0.2224	-0.1577	0.5517	0.4853	0.3801	0.2427265910	13
216	0.0855	0.0855	0.1873	0.1873	-0.0596	-0.0596	0.0000	0.0000	0.0000	0.0000000000	1
217	0.1574	0.0746	0.0961	0.0534	0.0464	-0.1717	0.0828	0.0427	0.2181	0.0018391624	2
218	0.1546	-0.4238	0.0834	-0.3640	0.1463	-0.3766	0.5784	0.4474	0.5229	0.3227372673	11
219	0.2632	-0.4238	0.2415	-0.4377	0.2224	-0.3766	0.6870	0.6792	0.5990	0.6666339819	40
220	0.3395	-0.4238	0.2415	-0.1881	0.2224	-0.1832	0.7633	0.4296	0.4056	0.3172222878	40
221	0.2130	0.1439	0.2105	0.0023	-0.1115	-0.1758	0.0691	0.2082	0.0643	0.0022063579	2
222	0.2632	0.0855	0.2415	-0.0501	-0.0092	-0.1717	0.1777	0.2916	0.1625	0.0200832745	5
223	0.0806	0.0806	0.1301	0.1301	0.0029	0.0029	0.0000	0.0000	0.0000	0.0000000000	1
224	-0.2247	-0.2885	0.0514	-0.1361	0.0333	-0.0690	0.0638	0.1875	0.1023	0.0029187964	2
225	-0.2247	-0.4238	0.0401	-0.1361	0.0626	-0.0690	0.1991	0.1762	0.1316	0.0110113170	3
226	0.1751	0.1751	-0.1003	-0.1003	0.0817	0.0817	0.0000	0.0000	0.0000	0.0000000000	1
227	0.2377	0.0450	0.0869	-0.1881	0.2224	-0.1797	0.1927	0.2750	0.4021	0.0508223442	6
228	0.2283	0.1300	0.2105	-0.1015	-0.0675	-0.1727	0.0983	0.3120	0.1052	0.0076953799	4
229	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
230	0.1651	0.0790	0.0981	-0.2438	0.1557	-0.0284	0.0861	0.3419	0.1841	0.0129259435	3
231	0.4230	0.2283	0.0714	-0.1848	0.2484	-0.1084	0.1947	0.2562	0.3568	0.0424498475	4
232	-0.1432	-0.1432	0.1086	0.1086	0.0062	0.0062	0.0000	0.0000	0.0000	0.0000000000	1
233	0.2130	0.2130	0.2105	0.2105	-0.1115	-0.1115	0.0000	0.0000	0.0000	0.0000000000	1
234	0.2283	0.2127	0.0636	-0.0501	-0.1084	-0.1132	0.0156	0.1137	0.0048	0.0000203064	2
235	0.3348	0.1685	-0.0166	-0.1848	0.2484	0.0525	0.1663	0.1682	0.1959	0.0130694974	5
236	0.1574	0.1574	0.0961	0.0961	-0.1717	-0.1717	0.0000	0.0000	0.0000	0.0000000000	1
237	0.3388	0.0044	0.2415	-0.1003	0.1578	-0.0284	0.3344	0.3418	0.1862	0.0507603041	9

Appendix 3. Environmental variables measured and ordination axis positions of the 92 plots. Abbreviations: Marg., marginal ridge; Pied., piedmont; Flat, flat highlands; Valley, secondary valley; Bott., bottomhill; Subw., subwet; Sat., saturated; Conc., concave endorreic; F. end., flat endorreic; Drain., drained; Bil.sl., bilateral symmetry in the slope direction; Bil.or., bilateral symmetry orthogonal to slope direction; Ellip., ellipsoid; Heter., heterometric radial symmetry; Water, water body; Grass, grassland; Sedge, sedge-rushland; Shrub, shrubland; M. Sav., man-made savanna; E. oaks, evergreen oaks; D. oaks, deciduous oaks; Pine, pine forest; Alpine, alpine shrubland; Veg. alt., vegetation altitudinal belt; Soil W., soil wetness; Cond., conductivity (microsiemens/cm); concentrations of Na, K, Ca, Mg, Cl, SO₄, CO₃H, NO₃, and P are in meq/L; O.M., organic matter; W. index, water index.

A tab-delimited version of this appendix is available as a [text file](#).

Plot	Morphotectonic units				Geomorphological units			Slope		Topographic position		
	Ridge	Marg.	Pied.	Slope	Flat	Valley	Basin	Pied.	Slope>4o	Bott.	Slope	Uphill
1	0	0	1	1	0	0	0	0	0	1	0	0
2	0	0	1	0	0	1	0	0	0	1	0	0
3	0	0	1	0	0	1	0	0	0	1	0	0
4	0	0	1	0	0	0	0	1	0	1	0	0
5	0	0	1	0	0	0	0	1	0	0	1	0
6	0	0	1	0	0	0	0	1	0	1	0	0
7	0	0	1	0	0	0	0	1	0	1	0	0
8	0	0	1	0	0	0	0	1	0	1	0	0
9	0	0	1	0	0	0	0	1	0	1	0	0
10	1	0	0	1	0	0	0	0	1	0	1	0
11	1	0	0	1	0	0	0	0	0	0	1	0
12	1	0	0	1	0	0	0	0	1	0	1	0
13	1	0	0	1	0	0	0	0	0	0	1	0
14	1	0	0	1	0	0	0	0	1	0	1	0
15	0	0	1	0	0	0	0	1	1	1	0	0
16	1	0	0	1	0	0	0	0	1	0	1	0
17	1	0	0	1	0	0	0	0	1	0	1	0
18	1	0	0	0	0	1	0	0	0	1	0	0
19	1	0	0	0	1	0	0	0	0	1	0	0
20	1	0	0	0	1	0	0	0	0	0	0	1
21	0	0	1	0	0	0	0	1	0	1	0	0

22	0	0	1	0	0	0	0	1	0	1	0	0
23	1	0	0	1	0	0	0	0	1	0	1	0
24	1	0	0	1	0	0	0	0	1	0	1	0
25	1	0	0	1	0	0	0	0	1	0	1	0
26	1	0	0	1	0	0	0	0	0	1	0	0
27	1	0	0	1	0	0	0	0	1	0	1	0
28	1	0	0	1	0	0	0	0	1	0	0	1
29	1	0	0	1	0	0	0	0	0	0	1	0
30	1	0	0	1	0	0	0	0	1	0	1	0
31	1	0	0	1	0	0	0	0	1	1	0	0
32	1	0	0	0	0	1	0	0	0	0	1	0
33	1	0	0	0	0	1	0	0	1	0	1	0
34	1	0	0	1	0	0	0	0	1	0	1	0
35	1	0	0	1	0	0	0	0	0	1	0	0
36	1	0	0	1	0	0	0	0	1	0	1	0
37	1	0	0	1	0	0	0	0	1	0	1	0
38	1	0	0	1	0	0	0	0	1	1	0	0
39	1	0	0	1	0	0	0	0	1	0	1	0
40	1	0	0	0	0	0	1	0	1	1	0	0
41	1	0	0	0	0	0	1	0	1	0	1	0
42	1	0	0	1	0	0	0	0	1	0	1	0
43	1	0	0	0	1	0	0	0	0	1	0	0
44	0	1	0	1	0	0	0	0	1	0	1	0
45	0	0	1	0	0	0	0	1	1	0	1	0
46	0	0	1	0	0	0	0	1	1	0	1	0
47	0	0	1	0	0	0	0	1	0	1	0	0
48	0	0	1	0	0	0	0	1	1	1	0	0
49	0	0	1	0	0	0	0	1	1	1	0	0
50	1	0	0	0	1	0	0	0	0	0	1	0
51	1	0	0	1	0	0	0	0	1	0	1	0
52	1	0	0	0	1	0	0	0	1	1	0	0
53	1	0	0	0	1	0	0	0	1	1	0	0
54	1	0	0	1	0	0	0	0	1	1	0	0
55	1	0	0	1	0	0	0	0	1	0	0	1
56	1	0	0	1	0	0	0	0	1	0	1	0
57	1	0	0	0	1	0	0	0	1	0	1	0
58	1	0	0	1	0	0	0	0	1	0	1	0
59	1	0	0	1	0	0	0	0	1	0	1	0
60	1	0	0	0	0	0	1	0	1	0	1	0
61	1	0	0	0	1	0	0	0	0	0	0	1
62	1	0	0	1	0	0	0	0	1	0	1	0
63	1	0	0	1	0	0	0	0	0	0	1	0
64	1	0	0	0	0	0	1	0	0	1	0	0
65	0	0	1	1	0	0	0	0	1	0	1	0
66	0	0	1	1	0	0	0	0	0	1	0	0
67	0	0	1	0	0	0	1	0	0	1	0	0
68	0	0	1	0	0	0	1	0	0	1	0	0
69	0	0	1	0	0	0	0	1	0	1	0	0
70	0	0	1	0	0	0	0	1	0	1	0	0
71	0	0	1	0	0	0	0	1	0	1	0	0
72	0	0	1	0	0	0	1	0	0	1	0	0
73	1	0	0	1	0	0	0	0	1	0	1	0
74	1	0	0	1	0	0	0	0	1	0	1	0
75	1	0	0	1	0	0	0	0	1	0	1	0
76	1	0	0	1	0	0	0	0	0	1	0	0
77	1	0	0	1	0	0	0	0	1	0	1	0
78	1	0	0	1	0	0	0	0	1	0	1	0
79	1	0	0	0	0	0	0	1	0	0	1	0
80	1	0	0	0	0	0	0	1	0	1	0	0
81	0	1	0	0	0	0	1	0	0	0	1	0
82	0	1	0	0	0	0	1	0	0	1	0	0
83	1	0	0	0	0	0	0	1	1	1	0	0
84	0	0	1	0	0	0	0	1	0	1	0	0
85	0	0	1	0	0	0	0	1	0	1	0	0
86	0	0	1	0	0	0	0	1	0	1	0	0
87	1	0	0	0	1	0	0	0	0	1	0	0

88	1	0	0	0	1	0	0	0	1	0	1	0
89	1	0	0	0	1	0	0	0	1	1	0	0
90	1	0	0	1	0	0	0	0	1	0	1	0
91	1	0	0	0	1	0	0	0	0	1	0	0
92	1	0	0	1	0	0	0	0	1	0	1	0

Appendix 4 Details of the multivariate methods used to determine the environmental volume of the species.

In each plot, we recorded 53 variables ([Appendix 3](#)) that were ultimately reduced into a three-dimensional, multivariate space. This reduction was done through a two-step, multivariate analysis. The first step consisted of reducing the 53 variables to 12 variables, several of which were multivariate composites.

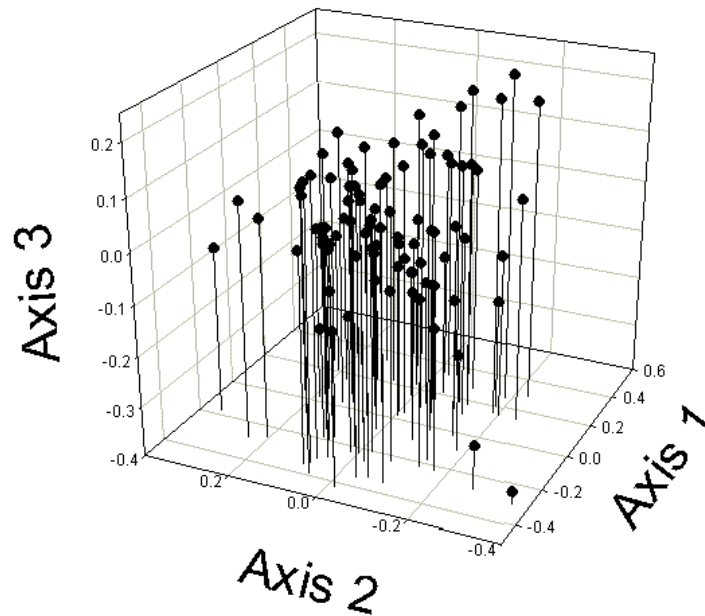
The first set of three composite variables were derived from 32 binary variables consisting of information on land form (type of morphotectonic unit and type of geomorphological unit), topography, drainage, grassland shape, vegetation physiognomy, and altitude zone. Land form variables were inferred from 1:50000 geological maps, and the rest of variables in this group were inferred from photo-interpretation of 1:20000 panchromatic stereopairs. Composite variables were derived from the first three eigenvectors of a correspondence analysis. These three eigenvectors primarily represented landscape position of the wet grasslands.

The next set of three composite variables consisted of the first three eigenvectors of a PCA based on soil chemical composition: pH, conductivity, sodium, potassium, calcium, magnesium, chloride, sulfate, carbonate and bicarbonate, organic matter, nitrate, nitrogen, and phosphorous. We took five 20-cm depth soil samples regularly distributed within each plot. These five samples were mixed into one composite sample for analyses of soil chemical composition and soil texture. The following soil chemical composition variables were analyzed in a 1:10 soil solution: pH, conductivity, sodium, potassium, calcium, magnesium, chloride, sulfate, carbonate, bicarbonate, and nitrate. Organic matter, nitrogen, and phosphorous were directly analyzed in the soil sample. These three eigenvectors were interpreted as total ion content, proportion of organic matter, and soil acidity.

The seventh composite variable was soil texture, based on the first eigenvector of a PCA of the percentages of sand, silt, and clay. The other five variables were: altitude, actual evapotranspiration, water index, ground slope, and soil wetness. Altitude was estimated with a calibrated altimeter in the field. Actual evapotranspiration and water index were inferred from interpolation of the region climate stations. Ground slope was estimated with a clinometer in the field. Soil wetness was estimated by means of an index based upon qualitative indicators such as gley traits and percentage of saturation. Across all variables, <1% of the data were missing, primarily texture (11%) and nitrate (9%). In these instances, we substituted the mean value for that variable.

These 12 variables defined an environmental space based on the first three eigenvectors from a PCA. This single space was then used to determine the volumes for all species. The distribution of the sites in the space is shown in [Fig. 8](#). All ordination analyses were done with PC-ORD (McCune and Mefford 1995).

Fig. 8. Distribution of the 92 plots in the first three dimensions of the ordination space defined by the 53 environmental variables.



The environmental volume of each plant species was measured by determining the maximum and minimum coordinates on all three axes. To do this, for each species on each axis we determined the sites containing that species with the largest and smallest axis scores. The volume was the rectangular solid containing these points. This measure is equivalent to the range volume of Burgman (1989) except that we did not standardize axis length. For species appearing in only one site, the volume was zero. Changing this volume to an arbitrarily chosen small value (e.g., 10% of the smallest two-site volume), would not change the analyses.

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